SPECIES-GROUPS IN CTENOPHTHALMUS (SIPHONAPTERA: HYSTRICHOPSYLLIDAE)

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SYNOPSIS

The genus *Ctenophthalmus* is divided into 20 species-groups (with 19 subgroups) which are defined and the species listed under each; a list of synonyms and other nomenclatural changes is also given.

INTRODUCTION

Ctenophthalmus Kolenati, 1856, containing some 170 species and subspecies (81 monotypic and 22 polytypic species) or nearly 10 per cent of all known fleas, is the largest genus of Siphonaptera. It would, therefore, be desirable to divide the genus into smaller units in order to group the various taxa phylogenetically and to facilitate identification of the species. In 1940, when the number of described forms was 94, Wagner (Z. Parasitenk. 11: 593–606) divided Ctenophthalmus into five genera (one consisting of two subgenera) on the study of the then known 46 Palaearctic species (30 monotypic and 16 polytypic) only. Smit (1953, Entomologist, 86: 21) remarked

that "Since it is preferable to stress the relationships of all members of this group, and considering the characters used by Wagner for the division, it would be better to regard his proposed genera as subgenera; in this category they will serve a useful purpose because the number of species contained in the genus *Ctenophthalmus* s. l. is so large that subdivision of the genus is most desirable on grounds of convenience". Wagner's generic concepts have been generally accepted in the sense of subgenera. Russian authors (e.g. Ioff & Scalon, 1954, Fleas of Eastern Siberia: 105) also state that Wagner's genera should at most be given subgeneric rank, although Ioff & Scalon (op. cit.) (and Ioff & Tiflov, 1954, Key to Aphaniptera of S.E. U.S.S.R.: 87) refer to the subgeneric names as those of groups.

I had tried to continue where Wagner left off, assuming that it would be feasible to erect some more subgenera for the species which Wagner had not dealt with or which had not been described at the time, but all I have been able to do is to form 20 species-groups (with 19 subgroups) which presumably represent phylogenetic units; II Ethiopian species are left as an ungroupable residue. The neutral term "group" is used to indicate a number of related taxonomic units or a single species which is markedly different from other species; it does not refer to a formal category and has therefore no nomenclatural significance. One could of course regard these species-groups as subgenera, but my objections to this are that (a) with the constant discovery of new species a number of the groups, as defined below, may have to be altered to a greater or lesser degree; (b) by assigning a subgeneric name and a type-species to a unit, one fixes its status more firmly than by referring to it as a species-group; any alteration in the concepts of units, if used as subgenera, may give rise to nomenclatural difficulties; (c) ideally the members of a subgenus should form a "natural" group, but we know as yet too little about the various species to ascertain that the units conform to this requirement.

To define units within a large genus like Ctenophthalmus is not easy, for one has to decide what actually constitutes a character of fundamental phylogenetic importance. As various characters may come into that category, the question is which to regard as being of prime importance. To base a division on one character only is obviously inadvisable, for one could arrive at three quite different units by using characters A, B or C. However, within the genus Ctenophthalmus there is no correlation of two or more characters which may be regarded as fundamental, and it is therefore not possible to form a relatively small number of major groups (subgenera). Some examples are: (a) all Ethiopian species possess an area communis in both sexes and a pronotal ctenidium of 16 spines—the same is true for members of the unrelated agyrtes-group, but the latter have an occipital chaetotaxy which is different from that of all Ethiopian species except vanhoofi; (b) all Ethiopian species lack a curved seta at the apex of the labial palp but this is also the case in the unrelated fissurus- and rettigi-groups; (c) the development of the mid-coxal sulcus is normally a generic character but in Ctenophthalmus the sulcus may be complete, slightly interrupted or entirely interrupted.

When a member of a group takes to an ecological niche or mode of life which is very different from that occupied by the other members of the group, and as a result

undergoes more or less drastic morphological changes, the relationships between this member and the others or the group tend to be obscured. Fleas of fossorial mammals, for example members of the gratus-subgroup (assimilis-group), illustrate this very clearly. The structure of the genitalia leaves no doubt that the gratus forms, which have become associated with mole-rats (Spalax), belong to the assimilisgroup (Figs. 87, 147*, cf. Figs. 85, 86, 146), but they differ from all other members of that group, which are parasites of Microtinae, by having on terga II-VII rounded spiracular fossae (Fig. 35) like those in other, but unrelated, species which are parasitic on Spalax; and a much reduced and almost Y-shaped spiracular fossa on tergum VIII (Fig. 35) (a reduction has also taken place in congener tenuistigmatus, a parasite of Microtus). Furthermore, fleas of Spalax are more hairy than those of other hosts, and members of the gratus-subgroup are likewise more setose, though less completely so, but instead of having more setae, for example, in the tergal main rows, a short row of setae occurs on the pronotum anterior to the main row (in all other species of the genus there is only one pronotal row of setae) and a rudimentary fourth genal spine, variable in size but smaller than the normal spines, is present in a number of specimens (Figs. 9, 10)—a very exceptional development.

The *gratus*-subgroup shows, for example, that the use of the shape of the spiracular fossae as a principal unit-character may give misleading results if insufficient atten-

tion is paid to the affinities of the genitalia.

The influence of a change of ecological niche on the morphology of the flea appears to affect the head, thorax and pregenital abdominal segments much more immediately than the genitalia. Of the male genitalia the phallosome seems more liable to morphological changes than segment IX (although there are some exceptions). In the female, the shape and especially the chaetotaxy of tergum VIII are apparently more stable than the structure of the genitalia, although variations in the genitalia are far less obvious than those of the male.

This paper is not a revision and only species showing certain group characteristics have been illustrated. The genus will be fully dealt with by Hopkins & Rothschild in the *Catalogue of the Rothschild Collection of Fleas*, **4**, where keys will also be given. I have not been able to examine the faunistic literature to the full extent and the geographical ranges given for each species may not always be exhaustive.

I have not seen specimens of the following: φ of arcanus Smit; bifurcus Ioff; caballeroi Barrera; chionomydis Ioff & Rostigayev; δ of crudelis Jordan; δ of dinormus Jordan; δ of engis Rothschild; expansus Traub; φ of hispanicus Jordan; hypanis s. l.; kazbek Tiflov; kirschenblatti Argyropulo; φ of nyikensis Smit; δ of olbius Jordan & Rothschild; quadratus Liu & Wu; shovi Rostigayev; φ of stenurus Jordan; φ of tertius Smit; wladimiri Isayeva-Gurvich; φ of yunnanus Jordan.

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For loans and gifts of specimens of *Ctenophthalmus* I am indebted to many of my colleagues; they all have my cordial thanks. Mrs A. M. Wright deserves my gratitude for much practical assistance.

^{*} Figures referred to in the text are contained in Plates 1-58 at the end of this number.

CHARACTERS OF TAXONOMIC IMPORTANCE

HEAD

I. Thickness of frontal wall—usually thin (Figs. 1, 3, 11), but often thicker in fleas parasitizing fossorial rodents, i.e. members of spalacis-, caucasicus-, triodontus-groups (Figs. 4, 13).

2. Frontal wall with small seta in notch just above oral angle—this is present in moratus-group (Fig. 12) and occasionally (though not as distinctly) in species of

other groups (Figs. 13, 14, 15).

3. Development of eye—the eye is vestigial in parasites of fossorial hosts and here belong e.g. members of the spalacis-, triodontus-, dilatatus-groups and of the gratus-subgroup (assimilis-group) (Figs. 4, 9, 10, 13). In the majority of species the eye is distinct (Figs. 1, 3) and in Ethiopian species (except triodontus-group) the eye is usually relatively well developed and dark (Fig. 12).

4. Length of labial palp—this palp is shortest, reaching to about the middle of the fore coxa, in some African species (particularis, stenurus, tertius, lycosius); the palp reaches to about two-thirds the length of fore coxa in all other African species and in assimilis-group, to three-quarters the length in all other species except for nivalis- and golovi-subgroups (nivalis-group), dolichus-, spalacis- and triodontus-groups in which the palp reaches to the apex, and in dolomydis-subgroup (nivalis-group) and dilatatus-group in which it reaches well beyond apex of fore coxa.

- 5. Chaetotaxy and shape of apical segment of labial palp—this segment bears ventro-anteriorly three very small setae the middle one of which is directed posteriorly in all species which have a ventro-posterior hooked seta (Figs. 20-24); the lower of these three setae is often fairly stout in members of the assimilis-group (Figs. 22, 23); the upper seta points downwards except in members of spalacis-, fissurus-, rettigi-groups and of all Ethiopian groups, in which this seta points forwards and downwards (Figs. 24-28). This segment bears ventro-posteriorly either two or three setae: when there are two setae, the upper is relatively well developed and hook-shaped while the lower seta placed immediately below the hook-shaped one is extremely minute and often barely visible even at ×1000 magnification (Figs. 20–24). These two setae occur in all Holarctic species with the exception of members of fissurus- and rettigi-groups (Fig. 25); when three bristles are present as in fissurus-, rettigi- and all Ethiopian groups (Figs. 25–28), the two upper ones are short and straight or almost so, while the lower seta is usually somewhat longer and more distinct than the corresponding one in the species with only two ventro-apical setae. In the species with a hooked ventro-posterior seta the apex of the segment is usually triangular (Figs. 20-24), in those with unmodified setae the apex is obtuse (Figs. 25-28).
- 6. Presence or absence of an area communis—this is a pale ovoid area where the walls of the antennal fossae of the two sides are partly fused (Fig. 18); this incipient trabecula centralis is situated behind the middle of the antenna and is usually rather difficult to see, even in well cleared specimens. The area communis is absent in both sexes of the parcus-group, present in females of all other groups and in males of the agyrtes-group, russulae-subgroup (nivalis-group), rettigi-group and all Ethiopian groups.

7. Occipital rows of setae—the first of the three rows consists of two setae in the Holarctic species (Figs. 1, 2, 3, 11) except in members of the spalacis-group which may have only one seta, in *dux*-group where sometimes three setae are present, and in the following Ethiopian species: cophurus, eximius, vanhoofi and particularis (Fig. 18) (in some other Ethiopian species this row may also consist of only two setae but then the number usually fluctuates between two and four). The middle row consists of two small upper setae and one large seta, well separated from the upper ones, in one Ethiopian species (vanhooft) and in Holarctic species (Figs. 1, 2) with the exception of the rettigi-, dilatatus-groups (Figs. 3, 11) and inornatussubgroup (fissurus-group) in which this row consists of two rather closely set setae as is also the case in particularis (Fig. 18), and in the spalacis-group (Fig. 4) where the number varies from 2-4, while there is only one seta in fissurus and turcicus; in the caucasicus-group the three setae of the middle row are equally spaced; in the Ethiopian species (with the exception of vanhooft and particularis) the middle row consists of 3-5 setae which form a distinct row (Figs. 12, 13). The posterior row consists of five (occasionally 4-7) setae of which the lowest is the longest.

8. Genal spines—first (anterior) genal spine always with parallel striation (Figs. I-18), second and third spines either with oblique (Figs. I, 3, 6-8, 12) or parallel striation. The latter type of spine occurs only in dolomydis (Figs. 2, 5), dilatatus (Fig. II), turcicus and fissurus. A type of striation (of middle and posterior genal spines) which is intermediate between the parallel and oblique types is found in gratus (Figs. 9, 10), dux, inornatus, and the spalacis-group (Fig. 4). The ratio of

length between the three spines is on average I: I:3: I:6.

The spines are usually sharply pointed but in parasites of fossorial rodents (*Spalax*, *Tachyoryctes*) they often have rounded tips (Fig. 13); these spines are frequently broken off in varying degrees in those fleas.

THORAX

9. Length of pronotum—the pronotum is dorsally shorter than the pronotal spines in dolomydis (Fig. 2) and dilatatus, about as long as these spines in the spalacis, caucasicus, fissurus, moratus and rettigi-groups (Fig. 3) as well as in gratus and olbius; in all other species the pronotum is at least somewhat longer than the pronotal spines.

10. Rows of setae on pronotum—there is only one row of pronotal setae but in the gratus-subgroup an incipient short row may be present in front of the main row.

II. Number of spines in pronotal ctenidium—there are usually 14, 16 or 18 spines in the pronotal ctenidium; in particularis (Figs. 18, 19) there are only 12 spines but in this species the ctenidium is modified. There are 14 spines in both sexes of dilatatus and dolichus, 16 in male 14 in female in caucasicus-, dux- and pseudagyrtes-groups, 16 spines in agyrtes-group, russulae-subgroup (nivalis-group), spalacis- and all Ethiopian groups (except particularis); 18 spines in male 16 in female in assimilis and nivalis-groups (except russulae-subgroup); 18 spines in both sexes in rettigi- and parcus-group and in the inornatus-subgroup (fissurus-group).

12. Arrangement of pseudosetae under mesonotal collar—in most species there are three mesonotal pseudosetae on each side, the upper two of which are placed near the dorsum and the lower a little below the middle of the collar (Fig. 42). A different, but not always constant, arrangement is found in the caucasicus-, dolichus-, dilatatus-, triodontus-, particularis-groups (Figs. 43-45) and in the gratus-subgroup (assimilis-group).

13. Chaetotaxy of metepimeron—in the majority of species there are about halfa-dozen setae on the metepimeron but in turcicus and members of the spalacis- and

triodontus-groups the number of setae is usually larger (up to about a dozen).

LEGS

14. Oblique sulcus of mid coxa—the sulcus is (a) complete (Fig. 29) in members of the agyrtes-, dolichus-, pseudagyrtes- and all Ethiopian groups (except eximius); (b) interrupted in the middle in various degrees (Fig. 31) in spalacis-, rettigi-, triodontus- and eximius-groups, in fissurus-subgroup (fissurus-group) and sometimes in specimens of gratus-group; (c) broken in upper part, forming double lines (Fig. 30) as in nivalis- and dolomydis-subgroups (nivalis-group), some subgroups of assimilis-group, caucasicus-, dilatatus-, dux-, inornatus- and parcus-groups.

15. Number of setal notches in hind tibial margin—the dorso-posterior margin of the hind tibia has seven notches, each normally bearing two setae in all species except in members of the triodontus-group which usually have eight (occasionally even nine) because of an extra notch between the penultimate one and the notch

above it.

16. Length of longest apical seta of second hind tarsal segment—the length of this seta varies, according to species, from not quite extending to the apex of the third

segment to reaching beyond the apex of the fourth segment.

17. Number of lateral setae of fifth hind tarsal segment—there are (a) three pairs of lateral plantar setae on the fifth hind tarsal segment in the majority of Holarctic species and in two Ethiopian species (eximius, arcanus); (b) three or four pairs—or three setae on one side of the segment and four on the other—in the spalacis- and triodontus-groups and in the following Ethiopian species: lycosius, singularis, evidens, bacopus, ansorgei, calceatus, ominosus, debrauwerei and luberensis; (c) four pairs in dux-group, expansus and caballeroi (pseudagyrtes-group) and in all Ethiopian species except the ones mentioned under (a) and (b).

ABDOMEN

18. Smoothness of pregenital abdominal segments—the posterior margins of terga I-VII and especially of sterna II-VII are very minutely and rather sparsely serrated in members of the evidens-group and in engis, eximius and cophurus. In all other

species of the genus these margins are smooth.

19. Downward extension of main rows of tergal setae—in the majority of species only one seta (the lowest) of the main row on each of terga II-VII is situated below the level of the spiracular fossa; exceptions are members of the caucasicus-, fissurus-, spalacis-, triodontus- and dilatatus-groups in which usually two (sometimes three or —in triodontus-group—even four) setae extend below the level of spiracular fossa at least on terga III and IV (usually on terga II-VII or VI).

- 20. Numbers of antesensilial setae—both sexes have three antesensilial setae on each side except for eximius which has three setae in the male but usually four (not infrequently three or five on one or even both sides) in the female.
- 21. Presence or absence of lateral setae on basal sternum—the basal sternum has a small number of lateral setae in both sexes of the following: spalacis- and dux-groups, dolomydis-subgroup and in golovi, turcicus and stenurus (3), also in an occasional specimen of eumeces; this patch of setae is found in the female sex only in members of the caucasicus- and rettigi-groups and in parvus, iranus, singularis, eximius, audax and edwardsi.
- 22. Pattern of striation of basal sternum—the cuticular ridges of this sternum may form (a) a parallel pattern as in golovi-subgroup (nivalis-group), most members of assimilis-group, parcus-, dolichus-, spalacis-, caucasicus-, fissurus-, dux-, rettigi-, pseudagyrtes-, atomus-, calceatus- and eximius-groups and in cophurus, eumeces and stenurus; (b) finger-print pattern which occurs only in the following Ethiopian species: triodontus-group and in atomus, olbius, smithersi, singularis, blandulus, phyris, devignati, vanhoofi, bacopus, debrauwerei, luberensis and arcanus; (c) a pattern which is intermediate between a parallel and finger-print one and in which the centre of the lateral surface of the sternum somewhat resembles a honeycomb—this is found in all species other than those mentioned under (a) and (b).
- 23. Shape of spiracular fossae—the shape of the spiracular fossa of the metepimeron corresponds on the whole with that of terga II–VII but it is always larger; the fossa of tergum VIII is—as in all fleas—different from the ones on the preceding terga. The following main types of fossae on metepimeron and terga II–VII can be distinguished: (a) circular or broad oval—these are found in the caucasicus, spalacis-, fissurus-, triodontus- and rettigi-groups and in the gratus-subgroup (assimilis-group) (Figs. 35, 36, 37, 41); (b) elongate, rounded apically and of subequal width over entire length—in dux-group (Fig. 40); (c) elongate, with a widened rounded apical part—in dolic.hus-group (Fig. 38); (d) halter-shaped in dilatatus-group (Fig. 39); (e) co nical, i.e pointed posteriorly—in all other groups (Figs. 32–34).

The fossa of tergum VIII is usually a Y- or V-shaped structure (Figs. 32–33), but much broadened in members of the assimilis-group (Fig. 34c, f) (except the gratus-subgroup (Fig. 35c, f), congener tenuistigmatus and pisticus-subgroup).

MALE

- 24. Setae anterior to spiracular fossa of tergum VIII—one or a few more setae are present in about 20 per cent of the known species but this occurrence is not a group character.
- 25. Shape of sternum VIII—the margin of sternum VIII is (a) ventrally emarginate, e.g. in the nivalis- and rettigi-groups (Figs. 48–50, 52) and in acanthurus; (b) ventroposteriorly drawn out into a triangular lobe in the pseudagyrtes-group (Fig. 53), eximius and cophurus; (c) of unusual shape as shown in figures of capriciosus (Fig. 62), pisticus (Fig. 57), dolichus (Fig. 55), dilatatus (Fig. 61) and dux (Fig. 63); (d) in all other species sternum VIII has a broadly rounded or obtuse posterior margin; (e) in calceatus and ansorgei (calceatus-group) the ventral margin has the appearance of being partially folded over (Fig. 59).

- 26. Presence or absence of area fusoria—the area fusoria is a triangular or semicircular dorsal area of fusion of the two sides of the apodeme of tergum IX in male fleas (Fig 64, a.f.); it is absent in the agyrtes-, caucasicus-, dolichus-, pseudagyrtes-, rettigi- and eximius-groups and in cophurus, ominosus, calceatus and ansorgei. In all other species the area fusoria is developed to a greater or lesser degree.
- 27. Internal ventral incrassation of corpus of clasper (Fig. 64, v.i.)—this incrassation is (a) absent in caucasicus-, parcus-, dux-, dilatatus- and dolichus-groups and in inornatus, pollex, acanthurus, eximius and debrauwerei; (b) long, narrow and horizontal in agyrtes-, spalacis- and triodontus-groups and in pisticus; (c) triangular in assimilis-, nivalis-, pseudagyrtes- and moratus-groups and in evidens, atomus, vanhoofi, cophurus and luberensis; (d) narrow and upright in rettigi-, calceatus- and eumeces-groups and in turcicus, ominosus, singularis, phyris and devignati.
- 28. Acetabular process—in the atomus-group this process is large and hyaline (Text-fig. 112), in all other species of the genus it is not or not markedly differentiated from the rest of the corpus of clasper.
- 29. Shape and chaetotaxy of fixed process of clasper—this process is either entire or divided by a sinus into two lobes, the lower (ventral) of which may also be sinuate. An undivided (or almost so) process is only found in members of the fissurus- and rettigi-groups (Figs. 100, 101, 105, 106) and in a number of Ethiopian species (Figs. 108–110, 113, 118, 121). In all other species the fixed process is sinuate in various degrees and in a number of forms of the agyrtes-group as well as in bifurcus (nivalis-group) the lower lobe is also sinuate (Figs. 73, 77, 78).

Chaetotaxy: There is usually only one acetabular seta; in the *rettigi*-group and *fissurus*-subgroup (*fissurus*-group) there are apparently two acetabular setae, the upper of which may well be a displaced lateral seta of the clasper (Figs. 100, 105, 106); in *dilatatus*—in which the clasper processes are strongly modified—there are about half-a-dozen setae occupying the position of a single acetabular one (Fig. 97). Apart from the acetabular seta and a number of marginal and submarginal short setae, the fixed process has two (occasionally 1 or 3) long setae in the *agyrtes*-, *rettigi*- and *eximius*-groups; in most other species there are 3–5 long setae. The lower (ventral) lobe of a sinuate fixed process bears a small apical seta (Figs. 66, 68—a.s.), except in *dolichus* (Fig. 96), *iranus* (Fig. 92), *dilatatus* (Fig. 97) and in certain Ethiopian species such as *calceatus*- and *eumeces*-groups (Figs. 116–119), *singularis* (Fig. 123) and *devignati* (Fig. 125).

30. Shape and chaetotaxy of movable process of clasper—basically the shape of this process appears to be elongate rectangular (as e.g. in Figs. 64–66); often, and usually partially, the process is widened or narrowed in varying degrees and the range of variations can be seen from Figs. 64–68, 70–103.

The chaetotaxy of the movable process is fundamentally the same in all species of a genus, but variations in number and position of the setae do of course occur quite frequently. In *Ctenophthalmus* the following groups of setae are found: (a) along the dorso-anterior angle of the process on the outer side are several (up to

about 20) short setae which are often basiconiform, the so-called sensilla (Figs. 64-68, s.a.); when the angle is not very prominent (the anterior margin gradually merging into the dorsal one), the sensilla are often more numerous and extend along the greater part of the margin (e.g. Figs. 65, 67, 95, 96); if the movable process is triangular and has a narrow apex, the sensilla are either situated at the apex (as in the agyrtes-group (Figs. 70–79)) or along the anterior margin (rettigi-group (Figs. 105, 106)); (b) at or just below the dorso-posterior angle are two slender setae of which at least the dorsal one is often curved upwards (Figs. 64-68, x); in species with a strongly modified movable process these two setae help to determine where the true dorsal margin ends and the posterior margin begins (e.g. Figs. 66, 68, 81); (c) a short distance below the two x-setae is a short seta with a usually blunt tip (Figs. 64-68, y); (d) at varying distances below the y-seta is found the lowest group at the posterior margin, consisting usually of four slender setae—hence this group has been termed here "tetrad setae" (Figs. 64-68, t.s.). There are never any other setae at or near the margin below the tetrad setae. In certain species the lower x-seta is situated below the y-seta and it may then sometimes join up with the tetrad setae (see Figs. 90, 92, 109, 113-115, 118, 119, 128-130). There are two tetrads in phyris and sometimes in eximius which normally has three such setae, which number also occurs in the spalacis-group (Fig. 98), dolomydis (Fig. 82), iranus (Fig. 92), moratus-group (Fig. 111) and cophurus (Fig. 121). More than four tetrad setae (5-7) are found in the calceatus-group (Figs. 116, 117), audax (Fig. 109), ominosus (Fig. 112), dilatatus (Fig. 97) and solutus (Fig. 77); (e) relatively few small setae are scattered over the upper half of the inner and outer surface of the movable process.

31. Fovea of movable process—the fovea can be markedly elongate, ovoid or circular, according to species and is apparently absent only in breviatus (Fig. 65), arvalis (Fig. 89), eximius (Fig. 120), triodontus (Fig. 108) and edwardsi (Fig. 110).

32. Surface structure of inner side of movable process—the surface of the inner

32. Surface structure of inner side of movable process—the surface of the inner side of the movable process is smooth in all species except in members of the atomus-group in which the lower part of the surface is densely spiculose.

- 33. Shape and chaetotaxy of sternum IX—the distal arm of sternum IX can be very short, of medium length or about as long as the proximal arm. Usually one of these types is characteristic for a certain group but there are several exceptions. A most unusual feature is the bifid structure of the distal arm in bifidatus (Fig. 73); other diversions from the normal straight, simple distal arm are found in capriciosus (Fig. 75), dux (Fig. 95), jeanneli, moratus (Fig. III), acunus and ominosus (Fig. II2). Some of the apical setae of the distal arm are spiniform in acanthurus (Fig. II5) and capriciosus (Fig. 75) only; in all other species the setae of sternum IX are slender and usually rather short.
- 34. Phallosome—the phallosome in Ctenophthalmus is of a relatively simple structure. With a few exceptions the lateral walls of the aedeagus are symmetrical; the exceptions are found in the following Ethiopian species; singularis (Fig. 186), vanhooft (Fig. 187), debrauwerei (Fig. 188), smithersi (Fig. 189) and devignati (Fig. 190). Posteriorly and/or ventro-posteriorly the lateral walls may form hook-

shaped structures (e.g. Figs. 133–136, 140, 145, 146, 151, 152, 158, 171, 173, 175–178) or a small lobe (Figs. 179, 180); in a number of species the lower part of the posterior margin forms a narrow band-like sclerotization (see e.g. Figs. 131-136). Dorsally the lateral wall may be expanded in various degrees, e.g. in the assimilis-group (Figs. 146-154), parcus-group (Figs. 155, 156); in certain species there is a dorso-posterior extension due to excessive length of the dorso-apical sclerite (Figs. 134, 139, 141, 162, 166-169, 189, 190). In the agyrtes-group the lateral wall often forms ventrally a lamella which may be smooth, striated or covered with scale-like spicules and is either hanging down or folded up according to species or to subspecies (Figs. 131-134, 138-140). In a number of species the ventro-anterior part of the lateral wall has a rather strong sclerotization which encircles an apparent opening in the wall—this is referred to as the ventro-basal sclerotization (Figs. 69, v. b. s., 142-144, 146-154, 163). The tubus interior (Fig. 69, t.i.) is fairly long in dux (Fig. 158), moratus (Fig. 171) and luberensis (Fig. 185), but in all other species it is short and straight; the tubus interior may bear dorsally a sclerotized outgrowth of various shapes according to species. Dorso-apically of the tubus interior lies the dorso-apical sclerite (Fig. 69, d.a.s.) which is shaped like an inverted Y; its narrow dorsal portion is variable in length (see e.g. Figs. 130-138 and Figs. 141, 142, 147, 162); this sclerite is large in orientalis (Fig. 153), dux (Fig. 158), spalacis-group (Fig. 160), rettigi-group (Figs. 164, 165), triodontus-group (Figs. 166-168), moratusgroup (Fig. 171) and devignati (Fig. 190). Below the dorso-apical sclerite are the two hamulae (Fig. 69, h.a.) which dorsally cover the sides of the tubus interior; these hamulae are often ill developed and membranous, but in some species they are quite distinct (e.g. Figs. 131-133, 140, 145, 160-165, 179). The lunular sclerite (Fig. 69, l.s.) is a slender curved structure but in dilatatus (Fig. 159) it has a dorsoanterior bulbous expansion; in some Ethiopian species this sclerite is rather long and often strongly curved (e.g. Figs. 173–175, 179). The dorsal lobe of the fulcrum (Fig. 69, d.l.f.) is fairly variable as can be seen from Figs. 131-190, but this is a species character rather than a group one. The aedeagal apodeme (Fig. 69, a.a.) is long and narrow in most species; exceptions are e.g. pollex (Fig. 152), moratus-group (Fig. 171), nyikensis (Fig. 177), phyris (Fig. 184), singularis (Fig. 186) and smithersi (Fig. 189).

FEMALE

- 35. Shape of sternum VII—the posterior margin of this sternum is always lobed and the following main types can be distinguished: (a) with a dorso-lateral lobe which may be rounded, triangular or obtuse (Figs. 193a, 194, 196, 197); (b) with a rounded or obtuse dorso-lateral lobe below which there is a smaller lobe (Figs. 191, 195, 199); (c) with a sinuate dorso-lateral lobe (Figs. 192, 200, 205, 206, 210); (d) with a dorso-lateral and a ventral lobe (Figs. 192, 198, 202).
- 36. Shape of posterior margin of tergum VIII—this margin is either broadly rounded and without a distinct sinus, although often with a small dorso-lateral lobe as in the Holarctic species and in some Ethiopian species (eximius (Fig. 206), cophurus and luberensis), or sinuate as in all other Ethiopian species.

- 37. Unciform sclerotization of tergum VIII—a single or double unciform sclerotization is present in most members of the assimilis-, spalacis- and eximius-groups (Figs. 196, 197), singularis and blandulus; in all other species the sclerotization is absent or inapparent.
- 38. Chaetotaxy of tergum VIII—the following groups of setae can be distinguished: (a) anterior to the spiracular fossa there are one or a few small setae in about a third of the known species, but this occurrence is not a group character; (b) on the latero-ventral part, above the preventral row, is a patch of setae (rarely reduced to one) of which the posterior ones are the longest; (c) a preventral row of usually five or six setae. The length and position of the last two setae of this row constitute an important character; they are submarginal in all Holarctic species (Figs. 191–200, 202–205) except for the rettigi-group (Fig. 201) while in the Ethiopian species they are marginal (Fig. 211) except for the moratus-, eximius-, particularis- and triodontus-groups and cophurus in which they are submarginal (in some Ethiopian species only the last seta is truly marginal). The last seta is placed above and close to the penultimate one in the nivalis-, assimilis- and spalacis-groups (Figs. 194–198); in all other species the last two setae are more or less in line with the others of the row. In the majority of species the last seta is shorter and stouter than the penultimate one; in the parcus- and rettigi-groups and in audax (triodontus-group) there is little difference between those two setae (Figs. 207, 208); (d) in most species there are 3–5 genital setae (e.g. Figs. 191–196), but a larger number occurs in the spalacis-, fissurus-, dux-, rettigi- and triodontus-groups (Figs. 197, 201, 203, 205, 207).
- 39. Sternum VIII—the following four main types of sternum VIII can be distinguished: (a) with a broad and rounded apex as in solutus (Fig. 193a), dux (Fig. 203), rettigi (Fig. 201), acuminatus, ruris, acanthurus, evidens, edwardsi and luberensis; (b) with a short and narrow sclerotized apex as in agyrtes- (except solutus), assimilis-, pseudagyrtes-, dolichus- and dilatatus-groups (Figs. 191, 192, 195, 196, 199, 200, 202) and in golovi, dolomydis (Fig. 198), russulae (Fig. 192), caucasicus, triodontus, audax (Fig. 207), eximius (Fig. 206) and cophurus; (c) with a relatively long and narrow sclerotized apex as in nivalis, nifetodes and orphilus (Fig. 194); (d) the sternum is well sclerotized over the whole of its length and has a narrow apex as in the spalacis- and fissurus-groups (Fig. 197), golovi, parcus (Fig. 208), dinormus and in about half the number of Ethiopian species. The base of sternum VIII is rather strongly sclerotized in members of the assimilis-, nivalis-, dilatatus- and parcus-groups (Figs. 194–196, 198, 199, 208).
- 40. Genital ducts—the ductus bursae can be shorter, about as long as, or longer than the dorsal pronotal spines; the length can vary within a group. In vanhoofi and debrauwerei (which might be grouped together) the bursa copulatrix is folded over the top part of the ductus bursae and the duplicatura vaginalis (in front of the ductus bursae) is much enlarged and often contains small dark sclerotizations (Fig. 212). The ductus obturatus is sometimes as long as the ductus spermathecae (Fig. 193) but both ducts are very often invisible in cleared specimens and e.g. in vanhoofi and debrauwerei only the ductus spermathecae could be seen

(Fig. 212). In *smithersi* the ductus spermathecae is relatively very broad for most of its length.

41. Spermatheca—in Ctenophthalmus there is relatively little variation in the shape of the spermatheca; typical examples are shown in Figs. 191, 193–196, 201, 204. A small or fairly small spermatheca is found in the spalacis- fissurus- and moratus-groups (Figs. 197, 210) as well as in dolomydis (Fig. 198), dinormus, parcus, acuminatus, eumeces, bacopus, engis and olbius. A distinct transition of bulga into hilla is absent in dux only (Fig. 203). The bulga is somewhat constricted dorso-posteriorly in the following Ethiopian species: phyris, vanhoofi, debrauwerei (Fig. 212), devignati, smithersi and in occasional specimens of ominosus (Fig. 211), calceatus, ansorgei and natalensis.

CTENOPHTHALMUS Kolenati

Ctenophthalmus Kolenati, 1856, Parasiten der Chiroptern, Brünn ed.: 33 (type species (by subsequent designation): bisoctodentatus Kolenati, 1863).

Typhlopsylla Taschenberg, 1880, Die Flöhe: 86 (partim).

Spalacopsylla Oudemans, 1906, Tijdschr. Ent. 49: liii.

Ctenophthalmus subgenus Neoctenophthalmus Wagner, 1930, Mag. Parasit., Leningr. 1:154 (type species (by monotypy): dilatatus Wagner, 1928). Syn. nov.

Euctenophthalmus Wagner, 1940, Z. Parasitenk. 11: 595 (type species: assimilis Taschenberg, 1880). Syn. nov.

Spalacoctenophthalmus Wagner, 1940, l. c.: 595 (type species: typhlus Motsch., 1840 (=spalacis Jordan & Rothschild, 1911)). Syn. nov.

Palaeoctenophthalmus Wagner, 1940, l. c.: 596 (type species: rettigi Rothschild, 1908). Syn. nov.

Ctenophthalmus subgenus Paractenophthalmus Wagner, 1940, l. c.: 602 (type species (by subsequent designation): dolichus* Rothschild, 1913; see Costa Lima and Hathaway, 1946, Monogr. Inst. Osw. Cruz 4: 216). Syn. nov.

Head semifracticipit. Frontal tubercle small, triangular. Frontal row consisting of five setae, exceptionally four or six; anterior to the lowest seta usually a small or minute seta present and this is sometimes situated in a notch in the frontal margin. Ocular row of three long setae, the upper of which is placed at margin of antennal fossa above eye. Postantennal region of head with three rows of setae, the first and/or second sometimes represented by only a single seta. Genal ctenidium horizontal or (less commonly) oblique, composed of three straight, (sub)parallel and backward/downward pointing spines; in members of the gratus-subgroup a rudimentary fourth spine is quite often present between the eye and the posterior genal spine. Genal process rather narrow (often broader in the female than in the male) and with a rounded or obtuse apex, clearly visible behind the posterior genal spine. Eye fairly well developed (but never with a very distinct cornea), reduced or vestigial. Trabecula centralis absent, but a number of species, either in one sex or in both sexes, with an area communis, i.e. a fusion of the walls of the antennal fossae, visible as a fairly large oval pale area demarcated by a dark line. Setae of antennal pedicel extending only over base of clava in male, while in the female they may reach to about the apex of the clava. Labial palp five-segmented, the apex reaching to a point from the middle of the fore coxa to beyond the fore trochanter; the apical segment bears anteriorly three minute subapical setae and posteriorly one minute and either one curved or two shorter straight setae.

^{*}Wagner mentions dolichus and dux as belonging to this subgenus and although he states that he had not seen specimens of dux he knew the species from the description.

Pronotum normally with one row of setae, about half-a-dozen each side; pronotal ctenidium straight (except in *particularis*), consisting of 12 (in *particularis* only), 14, 16 or 18 spines which on the whole are at least as long as the pronotum. Mesonotum with three (in certain species four) pseudosetae each side under the collar. Metanotal pleural arch and ridge well-developed.

Mid coxa with the oblique pale sulcus either complete or interrupted. Tibae without a comb-like arrangement of marginal setae. Posterior margin of hind tibia normally with seven notches, each containing not more than two short setae (apical notch excepted). Fifth tarsal segments with a basal plantar pair, three lateral pairs on fore and mid tarsus and three or four pairs on hind tarsus.

First four terga on each side with usually only one marginal spinelet (exceptionally one only on tergum V also). Both sexes with three antesensilial setae each side (except in females of *eximius* and *hoogstraali* which normally have four antesensilials each side), of which the middle one is the longest. Sensilium with 17 trichobothria each side and with one seta at the posterior margin.

Male: Apodeme of tergum IX well developed; clasper with two minute setae and one leucodisc situated below the sensilium; manubrium usually fairly narrow and with an upturned tip; one acetabular seta (absent in dux- and dolichus-groups); fixed process of clasper usually divided into two lobes, the lower of which may be sinuate. Movable process without spiniform setae; with sensilla dorso-anteriorly or apically. Distal arm of sternum IX normally a straight simple structure; one or two of the apical setae of this arm thickened in only a few species.

Aedeagus structurally relatively simple: tubus interior short and straight; dorso-apical sclerite triangular and often elongate; hamulus usually feebly sclerotized; lateral wall of aedeagus sometimes lobed posteriorly or ventrally and the two sides asymmetrical in some species; aedeagal apodeme narrow in most species (never exceptionally broad); aedeagal tendons not making more than half a convolution.

Female: Sternum VIII with at least one lateral lobe. Tergum VIII with at most one seta at the posterior margin on the outer side. Sternum VIII varying in width, never very broad. Anal stylet with one long apical seta and two small subapical ones on the outer side. Ductus bursae not strongly sclerotized; ductus obturatus fairly long. Spermatheca normally with a barrel-shaped bulga which is clearly demarcated from the narrow hilla (except in dux); hilla without papilla.

agyrtes-group

Head (Fig. 1). Area communis present in both sexes. Eye clearly indicated. First genal spine shorter and narrower than second; ratio of spines 1:1·3:1·6. Labial palp reaching to $\frac{3}{4}$ length of fore coxa; with a curved apical seta. Anterior occipital row of two setae, middle row of three, interspace between most dorsal seta and middle seta smaller than that between latter and most ventral one.

Thorax. Pronotum shorter than length of pronotal spines. Pronotal ctenidium with 16 spines in both sexes. Arrangement of pseudosetae under mesonotal collar normal (Fig. 42). About half-a-dozen setae on metepimeron.

Legs. Sulcus of mid coxa complete. Longest apical seta of second hind tarsal segment reaching about to apex of third segment (except in apertus-subgroup of agyrtes-group, in which it reaches about to middle of fourth segment). Three pairs of lateral plantar setae on fifth hind tarsal segment.

Abdomen. Spiracular fossae of metepimeron and terga II-VII conical, that of tergum VIII Y-shaped (Figs. 32, 33). One seta (the lowest) of tergal main rows below level of tergal spiracular fossae. Basal sternum without lateral setae.

Male (Figs. 46, 47, 62, 68, 70–79, 131–140). Sternum VIII (Figs. 46, 47) with a smooth, rounded or broadly truncate posterior margin (except in capriciosus; see Fig. 62). Apodeme of tergum IX without an area fusoria (except in the bisoctodentatus-subgroup; see Fig. 79). Corpus of clasper with a horizontal internal ventral incrassation. Fixed process of clasper

divided by a triangular sinus into two lobes, the lower (ventral) of which may be subdivided by a sinus which is usually much broader than deep. Dorsal lobe of fixed process with two long marginal setae (except in solutus (Fig. 77) and bisoctodentatus (Fig. 79), which have 3-5 such setae). Ventral lobe of fixed process with a small dorso-apical seta. Movable process elongate, often triangular, gradually tapering towards the usually narrow apex along which about half-a-dozen sensilla are situated. Fovea elongate. Four tetrad setae (except in solutus, which has 7-9) situated usually well below apex of movable process. Distal arm of sternum IX very short in bisoctodentatus, of medium length in hispanicus (Fig. 71) and about as long as proximal arm in remaining species; apex of distal arm with at least a few of its setae longish except in bisoctodentatus which has only short setae; two of the setae subspiniform in capriciosus. Aedeagus (Figs. 131–140) without a dorsal expansion and without a ventro-basal sclerotization; aedeagal apodeme narrow.

Female (Figs. 191, 193). Sternum VII with a well-developed dorsal lobe below which often a smaller lobe. No setae anterior to spiracular fossa of tergum VIII (except in apertus). Posterior margin of tergum VIII broadly rounded, dorsally with a smallish lobe. Tergum VIII anteriorly without unciform sclerotization. Apical short and stout seta of preventral row of tergum VIII well separated from penultimate seta, not placed above the latter. Sternum VIII with a short and fairly narrow apex (subapical portion broader in solutus (Fig. 193a)); base of sternum VIII not strongly sclerotized. Ductus bursae at most as long as dorsal spines of

pronotal ctenidium. Spermatheca of normal shape and size; hilla shorter than bulga.

Distribution. Europe and Asia Minor.

Hosts. Muridae, especially Apodemus, except for bisoctodentatus which is a parasite of Talpa.

The group can be divided into the following seven subgroups:

agyrtes-subgroup

Male (Figs. 70, 71, 131, 132). Dorsal lobe of fixed process of clasper with two long and several shorter setae; broad ventral lobe entire or in varying degrees subdivided by a sinus. Distal arm of sternum IX of medium length or about as long as proximal arm, varying from narrow to fairly broad. Phallosome: dorso-apical sclerite not very long; hamulus rectangular, fairly well differentiated; lateral wall ventro-posteriorly with marginal sclerotization and ventrally with a distinct lobe which may be smooth, striated, scaled and turned up or down and does not extend to ventro-posterior part of lateral wall.

Female. Posterior margin of sternum VII with a fairly large rounded dorsal lobe below

which usually a very small lobe.

agyrtes agyrtes (Heller, 1896), Ent. Nachr. 22: 97, figs. 1, 2 (as Typhlopsylla). Frisian islands, north-east Netherlands, northern Germany, Denmark, Poland except south-east, western half of Czechoslovakia and north-east Austria.

agyrtes dinarus Rostigayev, 1959, Zool. Zh. 38:779, 781, fig. 4. Jugoslavia. agyrtes eurous Jordan & Rothschild, 1912, Novit. 2001. 19:59, fig. 1. Romania. agyrtes fennicus Peus, 1950, Syllegomena biol., Wittenberg: 290, fig. 3b. Finland. agyrtes graecus Jordan, 1926, Novit. zool. 33: 392, fig. 19. Greece.

agyrtes impavidus Jordan, 1928, Novit. 2001. 34: 174, fig. 1. Northern and eastern France, northern Switzerland, Italy (Dolomites), Austria except the north-east. agyrtes kleinschmidtianus Peus, 1950, Syllegomena biol., Wittenberg: 295, fig. 5.

South-east Poland.

agyrtes ohridanus Wagner, 1939, Bull. Soc. sci. Skoplje 20: 163, figs. 3-5. Jugoslavia. agyrtes pelikani Rosický, 1959, Acta Acad. Sci. czechoslov. brun. 31: 328, fig. 4. Central Bulgaria.

agyrtes peusianus Rosický, 1955, Zool. ent. Listy 4:366, 378, 381, figs. 1a, 2. Czechoslovakia (Low Tatra).

agyrtes prothelenus Peus, 1958, Mitt. zool. Mus. Berl. 34: 156, figs. 16-19. Greece.

agyrtes provincialis Rothschild, 1910, Ent. mon. Mag. 46: 207, fig. 3 (\circ on p. 255). South-east France, south-west Switzerland.

agyrtes ropotamensis Rosický, 1959, Acta Acad. Sci. czechoslov. brun. 31: 329, figs. 5–9. South-east Bulgaria.

agyrtes rugosus Peus, 1959, Mitt. zool. Mus. Berl. 35: 93, figs. 2, 3. Sicily.

agyrtes sardiniensis Ioff, 1927, Ann. Mus. zool. Acad. St. Pétersb. 28: 428, fig. 12. Sardinia.

agyrtes serbicus Wagner, 1930, Acta Soc. ent. Jugoslav. 3–4: 38, 42, fig. 3. Jugoslavia. agyrtes smitianus Peus, 1950, Syllegomena biol., Wittenberg: 297, fig. 7E. Western and southern Netherlands, northern Belgium, southern Germany.

agyrtes taygetus Peus, 1958, Mitt. zool. Mus. Berl. 34: 157, figs. 20-23. Greece.

agyrtes verbanus Jordan & Rothschild, 1920, Ectoparasites 1:102, figs. 88, 89. Switzerland, northern Italy.

agyrtes wagnerianus Peus, 1950, Syllegomena biol., Wittenberg: 290, fig. 3C. Jugoslavia (north-western Slovenia).

hispanicus Jordan, 1938, Novit. 2001. 41: 108, fig. 50. Spain.

nobilis nobilis (Rothschild, 1898), Novit. 2001. 5:539 (as Typhlopsylla). South-east England, central and south-eastern France.

nobilis dobyi Beaucournu, 1962, Bull. Soc. zool. Fr. 87: 235, figs. 1–3. Pyrénées Orientales. France.

nobilis vulgaris Smit, 1955, Trans. R. ent. Soc. Lond. 107: 349, figs. 32–70. British Isles (except south-east England), western France.

andorrensis-subgroup

Male (Figs. 72, 73, 133, 134). Dorsal lobe of fixed process with two long and several shorter setae; broad ventral lobe not deeply sinuate. Tetrad setae of movable process situated rather high up in bifidatus (Fig. 73). Distal arm of sternum IX about as long as proximal arm, narrow (in bifidatus (Fig. 73) with, on each side, a ventro-basal extension bearing two long setae—a structure unique in the genus). Phallosome: dorso-apical sclerite as in members of agyrtes-subgroup; hamulus broad and crescentic in andorrensis (Fig. 133), not well sclerotized in bifidatus (Fig. 134); lateral wall ventro-posteriorly drawn out into a sharp projection, with only a very narrow strip of marginal sclerotization, and ventrally with a large triangular lobe which is either striated or scaled and reaches ventro-posterior part of lateral wall.

Female (Fig. 191). Sternum VII as in agyrtes-subgroup. Tergum VIII with usually only two genital setae (usually 3 or 4 in other subgroups).

two genital secae (usuany 3 of 4 in other subgroups).

andorrensis Smit, 1960, Proc. R. ent. Soc. Lond. (B) 29: 14, figs. 1–3. Andorra. bifidatus Smit, 1960, Tijdschr. Ent. 103: 277, figs. 1–3. Turkey.

arvernus-subgroup

Male (Figs. 47, 62, 74, 75, 135, 136). Posterior margin of sternum VIII strongly convex in arvernus (Fig. 47), more straight in baeticus and with a long slender projecting dorso-posterior lobe in capriciosus (Fig. 62) which is unique in the genus. Dorsal lobe of fixed ENTO. 14, 3. 2.

process of clasper with one or two long and several shorter setae; ventral lobe very narrow; acetabular seta very variable in length. Apex of movable process very narrow, with five minute sensilla. Distal arm of sternum IX about as long as proximal arm, with relatively few setae which are all placed at or near the apex, in *capriciosus* (Fig. 75) with two dorsal pre-apical subspiniform setae each side. Phallosome: dorso-apical sclerite short; hamulus rectangular; lateral wall ventro-posteriorly with a fairly broad marginal sclerotization (as in *agyrtes*-subgroup) with its tip extending well beyond the lateral wall, which forms ventrally at most a medium-sized smooth lobe.

Female. Sternum VII and segment VIII virtually as in the agyrtes-subgroup (cf. Fig. 191). arvernus Jordan, 1931, Novit. zool. 36:225, fig. 1. Southern France, northern Spain.

baeticus Rothschild, 1910, Ent. mon. Mag. 46: 208, figs. 1, 2. Portugal. capriciosus Smit, 1960, Tijdschr. Ent. 103: 279, figs. 4–7. Jugoslavia.

proximus-subgroup

Male (Figs. 76, 137). Dorsal lobe of fixed process with two long and several shorter setae; ventral lobe rather broad, undivided. Distal arm of sternum IX a little shorter than proximal arm, broad, with obtuse apex; proximal arm markedly straight. Phallosome: dorso-apical sclerite longish, triangular; hamulus poorly sclerotized; posterior margin of lateral wall without strong sclerotization, ventro-posteriorly with a short downward-pointing lobe; ventrally the lateral wall does not form a lobe.

Female. Sternum VII with a large rounded lateral lobe. Segment VIII as in the agyrtessubgroup. Ductus bursae about as long as dorsal pronotal spines.

proximus (Wagner, 1903), Horae Soc. ent. ross. 36: 147, Pl. 2, fig. 5 (as Typhlopsylla). Caucasus, Turkey.

solutus-subgroup

Male (Figs. 77, 138). Short dorsal lobe of fixed process of clasper with three long and several shorter setae; ventral lobe trapezoidal, very broad apically. Movable process with 7–9 tetrad setae. Distal arm of sternum IX triangular, about as long as proximal arm. Phallosome: dorso-apical sclerite very short; hamulus narrow, elongate; apical margin of lateral wall straight, slightly thickened in ventral half; lateral wall ventrally forming a very short lobe beneath which is a characteristic longitudinal sclerotization.

Female (Fig. 193). Posterior margin of sternum VII forming a very straight-edged broad lobe below which there may be a small sinus. Apex of sternum VIII broader than in the other subgroups.

solutus solutus Jordan & Rothschild, 1920, Ectoparasites 1:105, figs. 94, 95. Switzerland, north Italy, Austria, Czechoslovakia, eastern Germany, Poland, southern Ukraine.

solutus siculus Peus, 1959, Mitt. zool. Mus. Berl. 35: 97, figs. 4, 6. Sicily.

apertus-subgroup

Male (Figs. 78, 139). Dorsal lobe of fixed process with two long and two or three shorter apical setae; ventral lobe long and narrow or broad and subdivided by a wide sinus. Movable process with a comparatively small acetabular part, anterior margin sloping back from about middle, the lower part consequently L-shaped. Distal arm of sternum IX not quite as long as proximal arm, narrow, its apical half of uniform width, the apical margin oblique with ventral

angle more pronounced than dorsal one and a characteristic notch just below the former. Phallosome: inner tube directed upwards at an angle of 45° in relation to long axis of median lamella, dorso-apical sclerite rather long, aedeagus markedly drawn out dorso-posteriorly and with concave dorsal margin; hamulus large but feebly sclerotized; posterior margin of lateral wall not strongly sclerotized, with a large striate ventral lobe which may be turned up or down and has part of its margin minutely serrate.

Female. One or a few setae anterior to spiracular fossa of tergum VIII. Sternum VII with a large dorsal lobe below which there may be a short lobe, while the ventro-posterior angle

is also drawn out into a lobe. Sternum VIII as in the agyrtes-subgroup.

apertus apertus Jordan & Rothschild, 1921, Ectoparasites 1:133, figs. 107, 108. South-eastern France.

apertus allani Smit, 1955, Ent. mon. Mag. 91: 145, figs. 1-3. Northern Spain and central France.

apertus gilcolladoi Wagner, 1939, Z. Parasitenk. 11:235, figs. 1, 3, 6. Central Spain.

bisoctodentatus-subgroup

Spiracular fossae of terga II-VII larger than in members of the foregoing subgroups (Fig. 33,

-cf. Fig. 32).

Male (Figs. 79, 140). Apodeme of tergum IX small, with an area fusoria. Dorsal lobe of fixed process of clasper with two to three long and a number of shorter setae, latter also present on outer lateral surface of this lobe; ventral lobe very broad, trapezoidal. Manubrium strongly turned upwards. Movable process with broad rounded apex. Distal arm of sternum IX very short, none of its setae very long. Phallosome: small in relation to clasper, differing considerably from that of members of the other subgroups by a subdorsal deep sinus in posterior margin of lateral wall; hamulus rectangular, well developed; ventral margin of lateral wall with a small upturned triangular lobe (difficult to see even in extremely good preparations); tip of median lamella pointing strongly upwards.

Female. Sternum VII either with only a broad upper lobe or with a sinus dividing off a

narrower upper and similar or broader lower lobe.

bisoctodentatus bisoctodentatus Kolenati, 1863, Horae Soc. ent. ross. 2: 35, Pl. 2 fig. 6. Southern Sweden, north and east Germany, Poland, European U.S.S.R., Finland, Czechoslovakia, Romania, Jugoslavia, Austria, Switzerland, France, Jersey.

bisoctodentatus heselhausi (Oudemans, 1914), Ent. Ber. Amst. 4: 139 (as Spalacopsylla). Great Britain, Belgium, west and south Germany, north-east Austria, northern Switzerland.

nivalis-group

Head (Figs. 2, 5, 6). Area communis present in both sexes in the russulae-subgroup, absent in male and present (though rather small) in female in golovi-, nivalis- and dolomydis-subgroups. Eye moderately well developed, except in dolomydis (Fig. 2) in which it is vestigial. First genal spine shorter and narrower than second; ratio of spines $1:1\cdot2:1\cdot5$, except in russulae-subgroup in which it is $1:1\cdot5:2$. Labial palp reaching to $\frac{3}{4}$ length of fore coxa in russulae-subgroup, to apex (or slightly beyond) in the other three groups; with a curved apical seta. Anterior occipital row of two setae, middle row of three, interspace between upper and middle setae smaller than that between middle and lower ones.

Thorax. Pronotum shorter than length of pronotal spines, considerably so in russulae. Pronotal ctenidium with 16 spines in both sexes in russulae-subgroup and in dolomydis-subgroup:

with 18 spines in male and 16 in female in *golovi*-subgroup and *nivalis*-subgroup. Arrangement of setae under mesonotal collar normal. About half-a-dozen setae on metepimeron.

Legs. Sulcus of mid coxa complete in russulae- and golovi-subgroups, dorsally interrupted in nivalis- and dolomydis-subgroups. Longest apical seta of second hind tarsal segment reaching apex of third segment in russulae-subgroup, tip of third or middle of fourth segment in nivalis- and dolomydis-subgroups, and from middle to apex of fourth segment in golovi-subgroup. Three pairs of lateral plantar setae on fifth hind tarsal segment.

Abdomen. Spiracular fossae of metepimeron and terga II-VII conical, that of tergum VIII Y-shaped. One seta (lowest of tergal main rows) below level of tergal spiracular fossae. Basal sternum with some lateral setae in golovi-subgroup and dolomydis-subgroup, without such setae in russulae-subgroup and nivalis-subgroup.

Male (Figs. 48-50, 54, 66, 80-84, 141-145). Posterior margin of sternum VIII smooth in russulae-, nivalis- and dolomydis-subgroups (Figs. 48-50), finely serrate in golovi-subgroup (Fig. 54); ventral margin of this sternum apically emarginate in varying degrees (emargination barely visible in Argyropulo's figure of kirschenblatti (Argyropulo, 1936, Konowia 15: 146) but he states "Das 8. Sternit ist von der ventralen Seite schwach ausgeschnitten."). Apodeme of tergum IX with an area fusoria. Corpus of clasper with a triangular internal ventral incrassation except in the russulae-subgroup (Fig. 83). Fixed process of clasper divided by a sinus into a dorsal lobe, which may be fairly large, and a narrow, usually non-sinuate and apically obtuse ventral lobe. Dorsal lobe of fixed process with two to four large setae and a number of shorter ones; ventral lobe with a small apical seta inserted at middle of apical margin in members of nivalis-subgroup (Figs. 66, 80, 81) and more dorso-apically in other members of the group. Movable process usually broad and basically of rectangular shape which may not be immediately apparent in forms in which the apical and/or ventral portions of the margin are strongly slanting. Three to eight sensilla situated along dorso-anterior angle of movable process. Fovea ovoid, medium sized to very small. Four tetrad setae, usually situated well below dorso-posterior angle of movable process; in nifetodes sspp. there are 4-6 tetrads (Figs. 66, 81). Distal arm of sternum IX of medium length, quite narrow in russulae-, nivalisand dolomydis-subgroups (Figs. 80-83), broader in golovi-subgroup (Fig. 84); none of the setae at apex of distal arm very long. Aedeagus with a more or less straight dorsal margin in goloviand dolomydis-subgroups (Figs. 144, 145), with a convexity in middle of dorsal margin in nivalissubgroup (Figs. 142, 143) and with dorso-apical expansion in russulae-subgroup (Fig. 141); with a well-developed ventro-basal sclerotization in nivalis- and dolomydis-subgroups (Figs. 142-144) only. Aedeagal apodeme narrow.

Female (Figs. 192, 194, 198). Sternum VII with a large triangular dorso-lateral lobe and with a small ventral lobe in dolomydis-subgroup (Fig. 198), with or without this ventral lobe in nivalis-subgroup (Fig. 194); in golovi-subgroup an additional median lobe; in russulae-subgroup (Fig. 192) margin of sternum VII as in dolomydis-subgroup (Fig. 198) except dorso-lateral lobe squarer and subventral sinus narrower. Tergum VIII with a few setae anterior to spiracular fossa in nivalis-, dolomydis- and golovi-subgroups (Figs. 194, 198), without such setae in russulae-subgroup (Fig. 192). Posterior margin of tergum VIII broadly rounded, without sinus. Tergum VIII anteriorly without unciform sclerotization. Short and stout apical seta of preventral row of tergum VIII well-separated from penultimate seta and not placed above it in russulae- and golovi-subgroups (Fig. 192) while in nivalis- and dolomydis-subgroups (Figs. 194, 198) these two setae are close together and the apical stout seta is placed above penultimate one. Sternum VIII with narrow apex; base of sternum VIII strongly sclerotized except in golovi-subgroup. Ductus bursae about as long as dorsal spines of pronotal ctenidium. Hilla of spermatheca about as long as bulga in dolomydis, shorter in all other members of the nivalis-group.

Distribution. Mountainous regions of Southern Europe, North Africa, and Caucasus area.

Hosts. Crocidura (russulae-subgroup), Citellus and other rodents (golovi-subgroup) and Microtinae (nivalis- and dolomydis-subgroups).

Remarks. This group occupies an intermediate position between the *agyrtes*-and the *assimilis*-groups. Though admittedly a somewhat heterogeneous taxon, the group contains species more closely related to one another than to members of the other two groups. The species which belong to the *nivalis*-group can be divided into the following four subgroups.

nivalis-subgroup

Area communis absent in male, present in female. Labial palp reaching at least to apex of fore coxa. Pronotal ctenidium with 18 spines in male, 16 in female. Basal sternum without lateral setae.

Male (Figs. 50, 80, 81, 142, 143). Ventral margin of sternum VIII apically deeply emarginate. Dorsal lobe of fixed process of clasper with three or four long setae and a number of shorter but strong setae. Distal arm of sternum IX with oblique apical margin. Phallosome: dorsal wall with a convex expansion developed in various degrees; dorso-apical sclerite narrow, very long, attached to a small semicircular sclerotization at dorso-posterior angle of lateral wall; hamulus narrow, membranous; the lateral wall forms ventro-apically two small lobes which partially overlap; posteriorly the lateral wall is at most feebly thickened; with a well-developed ventro-basal sclerotization.

Female (Fig. 194). Posterior margin of sternum VII with a triangular dorso-lateral lobe. One or a few small setae anterior to spiracular fossa of tergum VIII.

Distribution. Mountainous areas in Switzerland, adjacent portions of Southern France, Germany, Austria and Italy, Jugoslavia, Pyrénées (one Q *orphilus* ssp. in Tring collection).

Hosts. Microtinae.

nivalis nivalis Rothschild, 1909, Novit. 2001. 16: 68, pl. 11, figs. 13, 14. South-east France (Hautes-Alpes and Haute-Savoie).

nivalis cervinus Jordan & Rothschild, 1920, Ectoparasites 1:100, figs. 85, 87. Switzerland.

nivalis helvetius Smit, 1963, Mitt. Schweiz. ent. Ges. 36: 100, figs 3, 4, 7. Switzerland. nifetodes nifetodes Wagner, 1933, Konowia 11: 279, fig. 5. Jugoslavia (Montenegro, Bosna).

nifetodes brelihi Rosický & Carnelutti, 1959, Čsl. Parasitol. 6: 140, 147, figs. 8–11. Jugoslavia (Slovenia).

nifetodes eugeniae Wagner, 1938, Konowia 16: 253, fig. 2. Jugoslavia (Hercegovina). nifetodes martinorum Smit, 1957, Ann. Mag. nat. Hist. (12) 10: 314, figs. 16, 17, 19, 22. Jugoslavia (Makedonija).

orphilus orphilus Jordan & Rothschild, 1923, Ectoparasites 1: 288, fig. 281. Switzerland, adjacent parts of southern France, Germany and Austria, not further east than about 11° 15′ E.

orphilus dolomiticus Jordan, 1928, Novit. 2001. 34: 175, fig. 3. Italy (Dolomites), parts of Austria and southern Germany not further west than about 11° 15′ E.

dolomydis-subgroup

Area communis absent in male, present in female. Eye vestigial. Labial palp reaching apex of fore coxa or slightly beyond. Pronotal ctenidium with 16 spines in both sexes. Basal sternum with some lateral setae.

Male (Figs. 49, 82, 144). Ventral margin of sternum VIII apically emarginate. Dorsal lobe of fixed process of clasper with three long and several shorter slender setae. Distal arm of sternum IX rather short, its apical margin oblique. Phallosome: dorsal wall of aedeagus straight, without an expansion; dorso-apical sclerite of medium length; hamulus not sclerotized and inapparent; ventro-apically the lateral wall forms one small lobe; posteriorly the lateral wall bears no sclerotizations; with a well-developed ventro-basal sclerotization.

Female (Fig. 198). Sternum VII with a large triangular lobe and a smaller ventral one.

A few small setae anterior to spiracular fossa of tergum VIII.

Distribution. Central Jugoslavia.

Host. Dolomys.

dolomydis Smit, 1957, Ann. Mag. nat. Hist. (12) 10: 317, figs. 20, 21, 23-26. Jugoslavia (Bosna).

russulae-subgroup

Area communis present in both sexes. First spine of genal ctenidium rather short. Labial palp reaching to about \(\frac{1}{4}\) lenth of fore coxa. Pronotal ctenidium with 16 spines in both sexes. Basal sternum without lateral setae.

Male (Figs. 48, 83, 141). Ventral margin of sternum VIII apically deeply emarginate. Dorsal lobe of fixed process with two long and a few shorter setae. Distal arm of sternum IX slender basally but broadening to oblique apical margin; proximal arm straight and narrow. Phallosome: dorso-apical sclerite much thickened and very long, hence dorsal wall of aedeagus forming a large triangular apical expansion; hamulus rectangular, not strongly sclerotized; ventro-apically the lateral wall forms a very small sharp lobe; lateral wall posteriorly not sclerotized; ventro-basal sclerotization virtually absent; aedeagal apodeme relatively wider than in other members of the subgenus.

Female (Fig. 192). Sternum VII as in dolomydis-group except dorso-lateral lobe squarer and subventral sinus narrower. No setae in front of spiracular fossa of tergum VIII.

Distribution. NORTH AFRICA, SARDINIA.

Host. Crocidura.

russulae Jordan & Rothschild, 1912, Novit. 2001. 19: 365, pl. 10, figs. 12, 13. Algeria, Sardinia.

golovi-subgroup

Area communis absent in male, present in female. Labial palp reaching apex of fore coxa. Pronotal ctenidium with 18 spines in male, 16 in female. Basal sternum with some lateral setae.

Male (Figs. 54, 84, 145). Ventral margin of sternum VIII apically emarginate in varying degrees, emargination almost absent in *kirschenblatti*. Dorsal lobe of fixed process of clasper with three long setae and several shorter ones. Distal arm of sternum IX fairly broad. Phallosome: dorsal wall of aedeagus straight, without an expansion; dorso-apical sclerite of medium length, narrow; hamulus quadrangular, well sclerotized, especially posteriorly; lateral wall ventro-apically drawn out into a sharp hook-like extension and posteriorly not sclerotized; without a ventro-basal sclerotization.

Female. Sternum VII with two or three lobes. A few small setae anterior to spiracular fossa of tergum VIII.

Distribution. CAUCASUS.

Hosts. *Citellus* and other rodents.

golovi golovi Ioff & Tiflov, 1930, Mag. Parasit., Leningr. 1: 215, 227. figs. 11, 12. Northern regions of Caucasus.

golovi alpestris Argyropulo, 1935, Z. Aserbeid. Inst. Microbiol. 5: 188, fig. 67(2). Azerbaidzhan.

bifurcus Ioff, 1940, Mag. Parasit., Leningr. 7: 219, 227, fig. 11. Middle Caucasus. chionomydis Ioff & Rostigayev, 1950, Med. Parazitol., Moskva 19: 271. Western

kirschenblatti Argyropulo, 1936, Konowia 15: 145, figs. 1, 2. Gruziya.

assimilis-group

Head (Figs. 7-10). Area communis absent in male, present in female. Eye moderately well developed except in gratus in which it is vestigial. First genal spine not very markedly shorter or narrower than second; ratio of spines 1: 1.2: 1.4 or 1.5, except in gratus-subgroup in which it is 1:1.2:1.7. Labial palp reaching to two-thirds or \frac{1}{4} length of fore coxa; with a curved pre-apical seta. Anterior occipital row of two setae, middle row of three and interspace between middle seta and upper one smaller than between former and lower one. Interspace between lowest and penultimate setae of the posterior occipital row not much larger than those between other setae of row.

Thorax. Pronotum shorter than or subequal to pronotal spines. Pronotal ctenidium with 18 spines in male and 16 in female in assimilis-, parvus-, orientalis- and pisticus-subgroups, in gratus- and breviatus-subgroups the number in female is 16 but in male it varies from 16-18, the former number being commoner in all species. Normal arrangement of pseudosetae under mesonotal collar, except in gratus sspp. which often have only one or two dorsal pseudosetae each side. About half-a-dozen setae on metepimeron.

Legs. Sulcus of mid coxa either complete or dorsally interrupted in varying degrees. Longest apical seta of second hind tarsal segment reaching to tip of third segment or to about middle of fourth. Three pairs of lateral plantar setae on fifth hind tarsal segment.

Abdomen. Spiracular fossae of metepimeron and terga II-VII conical, except in gratus (Fig. 35) in which they are more or less circular; spiracular fossa of tergum VIII of female broad (much reduced in gratus, congener tenuistigmatus and Y-shaped in pisticus). One seta (the lowest of the tergal main rows) below level of tergal spiracular fossae. Basal sternum with a few lateral setae in only the female of a few species; cuticular ridges of this sternum not forming a finger-print pattern.

Male (Figs. 51, 56, 57, 64, 65, 69, 85-94, 146-154). Sternum VIII with a broadly rounded posterior margin which is at least partially finely serrate. Apodeme of tergum IX with an area fusoria. Corpus of clasper with a triangular internal ventral sclerotization. Fixed process of clasper with a usually large dorsal lobe and a short ventral lobe which is always rather narrow, while it is not differentiated in arvalis and orientalis. Dorsal lobe of fixed process with 3-5 large marginal or submarginal setae; ventral lobe with a small dorso-apical seta, except in iranus (orientalis-subgroup). Movable process of a basically elongate rectangular shape, often narrowed in lower half; with 5-10 sensilla along dorso-anterior angle. Fovea ovoid or circular. Four tetrad setae (except in iranus which has 3), situated well below dorso-posterior angle which is usually markedly sclerotized. Distal arm of sternum IX rather broad and obtuse and of medium length (except in pollex in which it is subequal to proximal arm). Phallosome: aedeagus with a dorsal expansion which may be broad, long and narrow, or very little developed; with a ventro-basal sclerotization; posterior margin not strongly sclerotized; aedeagal apodeme narrow (except in pollex).

Female (Figs. 195, 196). Sternum VII usually with a squarish dorsal lobe, below which often a smaller rounded lobe. No setae anterior to spiracular fossa of tergum VIII (except in breviatus-subgroup, iranus, pisticus and wagneri). Posterior margin of tergum VIII broadly rounded, dorsally often with a small lobe. Tergum VIII anteriorly with a single or double unciform sclerotization in assimilis- and orientalis-subgroups. Apical short and stout seta of preventral row of tergum VIII situated very close to and above penultimate seta. Sternum VIII with a narrow apex; base of sternum VIII strongly sclerotized in several species. Ductus bursae at most as long as dorsal pronotal spines in assimilis- and pisticus-subgroups, longer in the other groups. Spermatheca of normal shape and size; hilla shorter than bulga.

Distribution. PALAEARCTIC REGION.

Hosts. Predominantly on Microtinae; orientalis-, pisticus-subgroup and a few members of the breviatus-subgroup on Sciuridae, while gratus has become a Spalax parasite.

This group can be divided into six subgroups.

assimilis-subgroup

Labial palp reaching to two-thirds length of fore coxa. Basal sternum of female normally without lateral setae.

Male (Figs. 69, 85, 86, 146). No setae anterior to spiracular fossa of tergum VIII. Dorsal lobe of fixed process of clasper large but not much differentiated, with three or four long setae and several shorter ones; ventral lobe short and obtuse. Distal arm of sternum IX short and broad, not or hardly tapering caudad, with a straight apical margin. Phallosome: aedeagus with a broad basal and large dorsal expansion; dorso-apical sclerite long and slender; hamulus not strongly sclerotized, narrow and curved forward; lateral wall ventrally with a tooth-like projection.

Female (Fig. 195). Posterior margin of sternum VII with a large, often blunt, dorsal lobe below which usually a smaller rounded lobe. Tergum VIII anteriorly with a single or

double unciform sclerotization. Ductus bursae shorter than dorsal pronotal spines.

Hosts. Microtine rodents.

assimilis (Taschenberg, 1880), Die Flöhe: 95, pl. 4 figs. 27a, b (as Typhlopsylla). bogatschevi Wagner & Argyropulo, 1934, Z. Parasitenk. 7: 288, figs. 8–10. Azerbaidzhan.

congener congener Rothschild, 1907, Novit. zool. 14:331, fig. 5.

congener allousei Hubbard, 1956, Iraq nat. Hist. Mus. Publ. (11): 3, fig. 2 (lower part). Iraq.

congener asiaticus Argyropulo, 1935, Z. Aserbeid. Inst. Microbiol. 5: 194, fig. 74(2). Transcaucasia.

congener bureschi Rosický, 1959, Acta Acad. Sci. czechoslov. brun. 31: 331, figs. 10, 12a. South-west Bulgaria.

congener geminus Peus, 1959, Mitt. zool. Mus. Berl. 35: 98, figs. 7, 8. Sicily.

congener italoscopus Peus, 1958, Mitt. zool. Mus. Berl. 34: 163, figs. 26 A-C. Greece. congener levadianus Peus, 1958, Mitt. zool. Mus. Berl. 34: 162, figs. 25 A, B. Greece. congener secundus Wagner, 1916, Trud. Mus. Tavr. Gub. Zemstva (1914): 5, fig. 4. Crimea.

congener tenuistigmatus Smit, 1960, Bull. Brit. Mus. (nat. Hist.), Ent. 8: 341, figs. 8, 9. Israel.

congener troilus Peus, 1954, Bonn. zool. Beitr., Sonderb. 1954: 126, figs. 11, 12. Greece.

congener vicarius Jordan & Rothschild, 1921, Ectoparasites 1: 135, figs. 110, 111. Romania.

congeneroides congeneroides Wagner, 1930, Annu. Mus. zool. Acad. St. Pétersb. 30: 537. Russian Far East, Korea, Japan.

congeneroides truncus Ioff & Scalon, 1950, Med. Parazitol., Moskva 19: 272. Sakhalin, Japan.

crudelis Jordan, 1932, Novit. 2001. 38: 269, fig. 25. Yunnan.

intermedius Argyropulo, 1935, Z. Azerbeid. Inst. Microbiol. 5: 194, figs. 73(3), 75B. Azerbaidzhan.

obtusus Jordan & Rothschild, 1912, Novit. zool. 19: 60, figs. 3, 4. Norway, Central Europe.

savii Jordan & Rothschild, 1921, Ectoparasites 1: 137, fig. 112. Italy.

tatianae Argyropulo, 1936, Konowia 15: 148, figs. 3, 4. Transcaucasia.

uncinatus (Wagner, 1898), Horae Soc. ent. ross. 31:590, pl. 9 fig. 24, pl. 10 fig. 29 (as Typhlopsylla).

gratus-subgroup

Eye vestigial. Labial palp reaching to $\frac{3}{4}$ length of fore coxa. First two genal spines separated by a small interspace; a fourth small or fairly large genal spine, situated above the third spine, present in *gratus gratus* (Figs. 9, 10) and *gratus elaeus*. Pronotum in some specimens with two rows of setae. One or two pseudosetae under mesonotal collar, the ventral one often absent. Tergal spiracular fossae oval or almost circular (Fig. 35), not conical as in members of the other subgroups of the *assimilis*-group.

Male (Figs. 87, 147). Modified abdominal segments and phallosome of same type as in

members of assimilis-subgroup.

Female. Tergum VIII anteriorly with or without an unciform sclerotization. Ductus bursae subequal to dorsal pronotal spines.

Hosts. Spalax spp.

gratus gratus Jordan & Rothschild, 1920, Ectoparasites 1:123, figs. 102, 103. Greece. gratus elaeus Peus, 1958, Mitt. zool. Mus. Berl. 34:160, figs. 24A–C. Greece. gratus menoetius Peus, 1954, Bonn. zool. Beitr., Sonderb. 1954:125, figs. 9D, E, 10B. Greece.

parvus-subgroup

Labial palp reaching to two-thirds length of fore coxa. Basal abdominal sternum of female with a few lateral setae.

Male (Figs. 88, 148). Modified abdominal segments similar to those of members of the assimilis-group. Phallosome: dorsal expansion of aedeagus apparently quite large (it is distorted in the only male available for study); dorso-apical sclerite very short; hamulus membranous; lateral wall ventrally without a sharp hook-like projection.

Female. Tergum VIII anteriorly without an unciform sclerotization. Ductus bursae shorter than dorsal pronotal spines. In other respects similar to females of the assimilis-

subgroup.

Hosts. Microtine rodents (parvus has also been found on Apodemus and, presumably accidentally, on Talpa).

parvus Argyropulo, 1935, Z. Aserbeid. Inst. Microbiol. 5: 194, figs. 72, 73(4). Caucasus.

shovi Rostigayev, 1948, Med. Parazitol., Moskva 17: 252, figs. 1-3. Gruziya.

breviatus-subgroup

Labial palp reaching to $\frac{1}{4}$ length of fore coxa. Pronotal ctenidium with 16 spines in female and 18 in male in *breviatus*—in other species of this subgroup (of which I have seen

insufficient material) 16 appears to be the usual number for male as well.

Male (Figs. 64, 65, 89, 90, 151, 152). Tergum VIII with one or a few short setae in front of the spiracular fossa. Dorsal lobe of fixed process of clasper not very large; ventral lobe developed in varying degrees, virtually absent in arvalis, fairly long in pollex. Movable process not markedly narrower in lower half. Distal arm of st. IX widening caudad. Phallosome: aedeagus with a long, narrow, upright expansion; dorso-apical sclerite short and broad; hamulus elongate and of rather irregular shape, not strongly sclerotized; ventro-posterior angle of lateral wall of aedeagus drawn out into a narrow projection; median lamella of aedeagal apodeme narrow, except in pollex, in which it is very broad.

Female. Tergum VIII anteriorly without an unciform sclerotization. Ductus bursae longer

than dorsal pronotal spines.

Hosts. Microtinae, but pollex and breviatus mainly on Citellus.

arvalis Wagner & Ioff, 1926, Rev. Microbiol., Saratov 5: 76, fig. N. S.E. European U.S.S.R.

breviatus Wagner & Ioff, 1926, Rev. Microbiol., Saratov 5: 75, pl. 2 fig. 4. S.E. European U.S.S.R.

kazbek Tiflov, 1953, Med. Parazitol., Moskva 22: 464. Caucasus.

pollex Wagner & Ioff, 1926, Rev. Microbiol., Saratov 5: 75, fig. L, pl. 2 fig. 3. S.E. European U.S.S.R.

teres Ioff & Argyropulo, 1934, Z. Parasitenk. 7: 160, figs. 16, 17. Armenia.

wladimiri Isayeva-Gurvich, 1948, Izv. Akad. Nauk. Azerb. S.S.R. 5: 89. Azerbaidzhan.

orientalis-subgroup

Labial palp reaching to two-thirds or $\frac{3}{4}$ length of fore coxa.

Male (Figs. 56, 91–93, 149, 150, 153). No setae anterior to spiracular fossa of tergum VIII. Dorsal lobe of fixed process of clasper large or fairly large; ventral lobe developed in varying degrees, virtually absent in orientalis, very long in wagneri. Movable process variable; three tetrad setae in iranus, four in the other species. Distal arm of sternum IX short. Phallosome: aedeagus with a low dorsal expansion in wagneri and orientalis, a larger one in iranus; dorso-apical sclerite very large in orientalis, of normal size in other species; hamulus rather large but hardly sclerotized and therefore indistinct; ventral area of lateral aedeagal wall striated longitudinally.

Female (Fig. 196). Tergum VIII anteriorly with a single or double unciform sclerotization.

Ductus bursae longer than dorsal pronotal spines.

Hosts. Microtinae; orientalis exceptional in occurring on Citellus. hypanis hypanis Ioff, 1950, Med. Parazitol., Moskva 19: 272, Caucasus. hypanis riciensis Ioff, 1953, Med. Parazitol., Moskva 22: 464. Gruziya. iranus iranus Argyropulo, 1935, Z. Aserb. Inst. Microbiol. 5: 193, figs. 71, 73(6).

Transcaucasus.

iranus persicus Smit, 1960, Bull. Brit. Mus. (nat. Hist.), Ent. 8: 341, figs. 10–13. Iran.

orientalis (Wagner, 1898), Horae Soc. ent. ross. 31:591, pl. 10 fig. 30 (as Typhlopsylla). East and central Europe from steppes north of Caspian Sea to East Germany and Austria.

wagneri wagneri Tiflov, 1927, C. R. Congr. antipest. U.R.S.S.: 272, figs. 1, 2. Caucasus area.

wagneri krym Ioff, 1953, Med. Parazitol., Moskva 22: 464. Crimea. wagneri schuriscus Ioff, 1940, Mag. Parasit., Leningr. 7: 218, fig. 10. Caucasus.

pisticus-subgroup

Labial palp reaching to \(\frac{3}{4}\) length of fore coxa.

Male (Figs. 57, 94, 154). Tergum VIII with one or a few setae in front of the spiracular fossa. Sternum VIII short, middle of posterior margin broadly concave. Dorsal lobe of fixed process of clasper well developed, as is the triangular ventral lobe. Distal arm of sternum IX long and of medium width. Movable process narrowed in lower half. Phallosome: aedeagus only a little expanded dorsally; dorso-apical sclerite narrow and fairly long; hamulus broad and short, feebly sclerotized; ventro-apical angle of lateral wall drawn out into a curved sharp process.

Female. Tergum VIII without an unciform sclerotization; with setae anterior to spiracular

fossa. Ductus bursae shorter than dorsal pronotal spines.

Hosts. Sciuridae.

pisticus pisticus Jordan & Rothschild, 1921, Ectoparasites 1:134, fig. 109. Siberia. pisticus pacificus Ioff & Scalon, 1950, Med. Parazitol., Moskva 19:271. Russian Far East.

parcus-group

Head (Figs. 14, 15). Area communis absent in both sexes. Eye vestigial. First genal spine a little shorter and narrower than the second; ratio of spines I: I·2: I·5 or I·6. Labial palp reaching to two-thirds or $\frac{3}{4}$ the length of the fore coxa; with a curved apical seta. Anterior occipital row of two setae, middle row of three and the interspace between the upper two is smaller than between the lower two.

Thorax. Pronotum shorter than length of pronotal spines. Pronotal ctenidium with 18 spines in both sexes. Normal arrangement of pseudosetae under mesonotal collar. About half-a-dozen setae on metepimeron.

Legs. Sulcus of mid coxa dorsally interrupted. Longest apical seta of second hind tarsal segment reaching to about the middle of the fourth segment. Three pairs of lateral plantar setae on fifth hind tarsal segment.

Abdomen. Spiracular fossae of metepimeron and terga II-VII conical, that of tergum VIII Y-shaped. One seta (the lowest of the tergal main rows) below the level of the tergal spiracular fossae. Basal sternum without lateral setae.

Male (Figs. 103, 104, 155, 156). Tergum VIII without setae anterior to spiracular fossa. Sternum VIII with a finely serrate rounded posterior margin. Apodeme of tergum IX with an area fusoria. Corpus of clasper with a small triangular ventral internal incrassation in C. formosanus only, the incrassation apparently absent in the other species. Fixed process of clasper divided by a shallow sinus into two short or very short lobes, the lower (ventro-posterior) of which is not sinuate. Dorsal lobe of fixed process with three or four long setae. Ventral lobe of fixed process with a small seta. Movable process roughly quadrangular, with only four longish basiconiform sensilla along the dorso-anterior angle. Fovea circular or oval. Four tetrad

setae, placed well below the sclerotized dorso-posterior angle. Distal arm of sternum IX very short or of medium length, with at least some of its setae longish. Aedeagus with a fairly small triangular dorsal expansion and without a ventro-basal sclerotization; dorso-apical sclerite with a long and narrow dorsal extension; aedeagal apodeme narrow and apically curved upwards.

Female (Fig. 208). Sternum VII with a well developed dorsal lobe. No setae anterior to the spiracular fossa of tergum VIII. Posterior margin of tergum VIII broadly rounded. Tergum VIII relatively very short and anteriorly with or without an unciform sclerotization. The apical seta of the preventral row of tergum VIII not much differentiated from the other setae and well separated from and not placed right above the penultimate seta. Sternum VIII well sclerotized over its entire length especially basally. Ductus bursae shorter than dorsal pronotal spines. Spermatheca small; hilla shorter than bulga.

Distribution. Eastern Asia.

Hosts. Microtine rodents, especially on Eothenomys.

dinormus Jordan, 1932, Novit. zool. 38: 288, fig. 47. Szechuan.

formosanus Svihla, 1942, Pan-Pacif. Ent. 18: 133, figs. 1-3. Formosa.

parcus Jordan, 1932, Novit. zool. 38: 286, 288, figs. 44-45. Szechuan.

quadratus Liu & Wu, 1960, Acta ent. sinica 10: 172, pl. 1, figs. 4-6, 10-12. Yunnan.

yunnanus Jordan, 1932, Novit. zool. 38: 287, fig. 46. Yunnan.

dux-group

Head. Area communis absent in male, present in female. Eye vestigial. First genal spine shorter and narrower than second spine; ratio of spines I: I·2: I·5. Labial palp reaching to \frac{2}{3} the length of the fore coxa; with a curved apical seta. Anterior occipital row of two, sometimes three, setae; middle row of three setae and the interspace between the upper two smaller than between the lower two.

Thorax. Pronotum somewhat shorter than length of pronotal spines. Pronotal ctenidium with 14 (occasionally 16) spines in both sexes. Normally only one or two subdorsal pseudosetae under mesonotal collar. About half-a-dozen setae on metepimeron.

Legs. Sulcus of mid coxa dorsally interrupted. Longest apical seta of second hind tarsal segment reaching to beyond the apex of the fourth segment. Four pairs of lateral plantar setae on fifth hind tarsal segment.

Abdomen (Fig. 40). Spiracular fossae of metepimeron and terga II-VII relatively small and longish, the one of tergum VIII Y-shaped (Fig. 40). One seta (the lowest of the tergal main rows) below the level of the tergal spiracular fossae. Basal sternum with one or a few lateral setae in both sexes.

Male (Fig. 63, 95, 158). Sternum VIII with a smooth, rounded posterior margin, ventro-apically with a small sharp projection (Fig. 63). Apodeme of tergum IX with an area fusoria. Corpus of clasper without an internal ventral incrassation. Fixed process of clasper divided by a deep and fairly narrow sinus into a triangular dorsal lobe bearing three to five large setae and a finger-like lower lobe with a longish apical seta. Acetabular seta absent. Movable process long and rather narrow, gradually tapering towards a narrow apex; with about 15 basiconiform sensilla along the dorso-anterior margin. Fovea absent. Four tetrad setae placed a little below the dorso-posterior angle. Distal arm of sternum IX as long as proximal arm, of unusual shape (Fig. 95) and with short setae only. Aedeagus without a marked dorsal expansion and basally only slightly sclerotized; dorso-apical sclerite large; lateral wall ventro-apically drawn out into an elongate blunt-tipped projection.

Female (Fig. 203). Sternum VII bilobed. A few short setae anterior to the spiracular fossa of tergum VIII. Posterior margin of tergum VIII broadly rounded. Tergum VIII anteriorly without an unciform sclerotization. The apical short and stout seta of the preventral

row of tergum VIII well separated from, and placed obliquely above, the penultimate seta. Sternum VIII with a short but fairly broad apex; base of sternum VIII not strongly sclerotized. Ductus bursae about as long as dorsal pronotal spines. Spermatheca of a rather unusual shape, without a sharp demarcation between hilla and bulga (Fig. 203).

Distribution. CENTRAL ASIA.

Host. Ellobius talpinus.

dux Jordan & Rothschild, 1915, Ectoparasites 1: 22, figs. 26, 27. Central Asia.

dolichus-group

Setae relatively very long and thin. *Head* (Figs. 16, 17). Area communis absent in male present in female. Eye clearly indicated. First genal spine shorter and narrower than second, third spine in female not markedly longer than second (it is in 3); ratio of spines 3 : 1 : 3 : 1 : 3 : 1 : 3 : 1 : 3 : 1 : 5. Setae of frontal row quite long, especially in male. Labial palp reaching to apex of fore coxa; with a curved apical seta. Anterior occipital row of two setae, middle row of three and the interspace between the upper two is smaller than between the lower two.

Thorax (Fig. 44). Pronotum shorter than length of pronotal spines. Pronotal ctenidium with 14 spines in both sexes. Arrangement of pseudosetae under mesonotal collar abnormal, see Fig. 44. About half-a-dozen setae on metepimeron.

Legs. Sulcus of mid coxa complete. Longest apical seta of second hind tarsal segment reaching to beyond apex of fourth segment. Three pairs of lateral plantar setae on fifth hind

tarsal segment, but dolichus quadrinus is stated to have four pairs.

Abdomen (Fig. 38). Spiracular fossae of metepimeron and terga II–VII small, elongate and somewhat constricted subapically (Fig. 38), the one on tergum VIII Y-shaped. One seta (the lowest of the tergal main rows) below the level of the spiracular fossae. Basal sternum

occasionally with one or a few lateral setae in the female only.

Male (Figs. 55, 96, 157). Sternum VIII posteriorly forming an elongate triangular poorly sclerotized lobe (Fig. 55). Apodeme of tergum IX without an area fusoria. Corpus of clasper without an internal ventral incrassation. Manubrium short. Fixed process of clasper divided into a broad upper lobe, bearing two to five long setae and a finger-like ventral lobe which lacks an apical short seta. Acetabular seta absent. Movable process elongate, not unlike the shape of a sugar-loaf; upper (anterior) acetabular portion straight (unique in the genus); with 15 or more mostly long and slender basiconiform sensilla along the dorso-anterior margin. Fovea circular or oval. Four tetrad setae, situated well below dorso-posterior angle of movable process. Distal arm of sternum IX of medium length and tapering apically, with at least some of its setae long. Aedeagus without a dorsal expansion and without a ventro-basal sclerotization; aedeagal apodeme narrow.

Female (Fig. 200). Posterior margin of sternum VII bilobed. One or a few short setae anterior to the spiracular fossa of tergum VIII. Posterior margin of tergum VIII broadly rounded. Tergum VIII anteriorly without an unciform sclerotization. The apical short and stout seta of the preventral row of tergum VIII well separated from and not placed above the penultimate seta. Sternum VIII with a short sclerotized narrow apex; base of sternum VIII not strongly sclerotized. Ductus bursae shorter than dorsal pronotal spines. Sperma-

theca normal, hilla shorter than bulga.

Distribution. ASIA (from Caspian Sea to Mongolia).

Hosts. Gerbillinae.

dolichus dolichus Rothschild, 1913, Ann. Mag. nat. Hist. 8(12): 539, pl. 14, figs. 1, 2. Turkestan.

dolichus bair Ioff, 1940, Mag. Parasit. Leningr. 7: 220, 228, figs. 13, 15. Transcaspia. dolichus idae Ioff, 1940, Mag. Parasit. Leningr. 7: 222, 228, fig. 14. Turkestan.

dolichus kysyl Ioff, 1953, Med. Parazitol., Moskva [22] (5): 463. Uzbekistan. dolichus quadrinus Ioff, 1953, Med. Parazitol., Moskva [22] (5): 463, Kirgizia. dolichus ursat Ioff, 1953, Med. Parazitol., Moskva [22] (5): 463. Turkestan. dolichus ustjurt Ioff, 1940, Mag. Parasit. Leningr. 7: 220, 228, fig. 12. Transcaspia.

dilatatus-group

Head (Fig. 11). Area communis absent in male, present in female. Eye vestigial. Spines of genal comb relatively short, the first a little shorter than the second; ratio of spines $3 \cdot 1 \cdot 1 \cdot 3 \cdot 1 \cdot 5$, $9 \cdot 1 \cdot 1 \cdot 3 \cdot 1 \cdot 4$. Labial palp reaching to well beyond the apex of the fore coxa; with a curved apical seta. Anterior occipital row and middle row of two setae each.

Thorax (Fig. 45). Pronotum dorsally longer than length of pronotal spines. Pronotal ctenidium with 14 spines in both sexes. Pseudosetae under mesonotal collar arranged as in

Fig. 45. About half-a-dozen setae on metepimeron.

Legs. Sulcus of mid coxa dorsally interrupted. Longest apical seta of second hind tarsal segment reaching to beyond the apex of the fourth segment. Three pairs of lateral plantar

setae on fifth hind tarsal segment.

Abdomen (Fig. 39). Spiracular fossae of metepimeron and terga II-VII small, longish and somewhat constricted in the middle, the one on tergum VIII Y-shaped (Fig. 39). One or two setae of the tergal main rows below the level of the tergal spiracular fossae. Basal sternum with some lateral setae in female only.

Male (Figs. 61, 97, 159). Sternum VIII abnormal, see Fig. 61; with a smooth posterior margin; tergum VIII with several small setae anterior to the spiracular fossa. Apodeme of tergum IX with a very small area fusoria. The corpus of clasper without an internal ventral incrassation; manubrium large. Dorsal lobe of fixed process with about half-a-dozen large setae; ventral lobe divided into a squarish (median) lobe, bearing the short apical seta and situated below the movable process, and a rounded ventral lobe with 4–6 marginal setae. Movable process quadrangular, with 15 or more basiconiform sensilla along the rounded dorso-anterior margin. Fovea elongate. Five tetrad setae, situated well below dorso-posterior angle of movable process. Distal arm of sternum IX of medium length but very broad, with short setae only. Aedeagus without a dorsal expansion and without a ventro-basal sclerotization; aedeagal apodeme straight and very narrow; lunular sclerite bulbiferous dorso-anteriorly (a most unusual modification).

Female (Fig. 199). Sternum VII with a lateral sinus dividing a large dorsal triangular lobe from a much smaller ventral one. A number of small setae anterior to the spiracular fossa of tergum VIII. Posterior margin of tergum VIII broadly rounded. Tergum VIII anteriorly without an unciform sclerotization. The apical stout seta of the preventral row of tergum VIII well separated from and not placed above the penultimate seta. Sternum VIII with a short and rather narrow apex; base of sternum VIII strongly sclerotized. Ductus bursae shorter than dorsal pronotal spines. Spermatheca of normal shape and size; hilla shorter than bulga.

Distribution. CENTRAL ASIA.

Host. Myospalax.

dilatatus Wagner, 1928, Annu. Mus. zool. Acad. St. Pétersb. 30: 27, fig. 7. Central Asia.

spalacis-group

Head (Fig. 4). Area communis absent in male, present in female. Frontal wall fairly thick. Eye vestigial. Genal spines rather stout and blunt, with a distinct gap between the first and the second spines; ratio of spines 3:1:1:2:1:5, 1:1:1:1:5. Labial palp reaching to 1:1:1:1:1:5. Labial palp reaching to 1:1:1:1:1:5. Anterior occipital row

of one or two setae, middle row of 1–4 setae. The interspace between the lowest and the penultimate setae of the posterior occipital row is not much larger than those between the other setae of the row.

Thorax. Pronotum dorsally about as long as pronotal spines. Pronotal ctenidium with 16 spines in *spalacis* and *jeanneli* (in the latter occasionally 17 or 18), with 18 spines in *gigantospalacis*. Normal arrangement of mesonotal pseudosetae. Metepimeron with more than ten setae.

Legs. Sulcus of mid coxa completely interrupted. Longest apical seta of second hind tarsal segment reaching from the middle to beyond apex of fourth segment. Three or four pairs of lateral plantar setae on fifth hind tarsal segment.

Abdomen (Fig. 36). Spiracular fossae of metepimeron and terga II-VII almost circular, that of tergum VIII Y-shaped (Fig. 36). More than one seta of tergal main rows below level of tergal spiracular fossae, at least on the anterior terga. Basal sternum with some lateral

setae in both sexes. Cuticular ridges of this sternum parallel.

Male (Figs. 98, 160). Sternum VIII with a finely serrate rounded posterior margin. Apodeme of tergum IX with an area fusoria. Corpus of clasper with a long and narrow horizontal internal ventral incrassation. Fixed process of clasper divided by a deep sinus into two lobes; the dorsal lobe bears 3–5 large setae, the ventral lobe with a small apical seta; acetabular seta often not quite marginal. Movable process relatively broad, wider dorsally than ventrally, with about 10–15 sensilla along the anterior margin. Fovea elongate. Three tetrad setae, situated well below the sclerotized dorso-posterior angle. Distal arm of sternum IX of medium length or about as long as proximal arm, with relatively large number of long slender setae. Aedeagus dorsally only slightly expanded; dorso-apical sclerite stout, with a relatively short upright finger-like projection; hamulus well sclerotized; median lamella of aedeagal apodeme narrow.

Female (Fig. 197). Posterior margin of sternum VII with a large triangular or squarish dorso-lateral lobe. Some small setae anterior to spiracular fossa of tergum VIII. Posterior margin of tergum VIII broadly rounded; tergum VIII with or without an unciform sclerotization; the short and stout apical seta of the preventral row placed obliquely above the penultimate seta of the row; 8–12 genital setae. Sternum VIII well sclerotized over whole of its length. Ductus bursae longer than dorsal pronotal spines. Spermatheca small, hilla about as long as bulga.

Distribution. Romania, Caucasus area, Kazakhstan.

Hosts. Spalax spp.

spalacis Jordan & Rothschild, 1911, Novit. zool. 18:82, fig. 8. Southern European part of U.S.S.R.

gigantospalacis gigantospalacis Ioff, 1929, Ber. mikrobiol. Staatsinst. Rostow (8): 40, figs. 3B, 5B, 6, 7. Gruzinskaya S.S.R.

gigantospalacis uralospalacis Tiflov & Usov, 1939, Rev. Microbiol., Saratov 17: 144, figs. 3, 4. Kazakhstan.

jeanneli Jordan. 1929, Novit. 2001. 35: 178, figs. 9, 10. Romania.

caucasicus-group

Head. Area communis absent in male, present in female. Frontal wall fairly thick. Eye vestigial. First genal spine almost as long as second; ratio of spines 1:1·2:1·5. Labial palp reaching to \(\frac{1}{4}\) length of fore coxa or to the apex; with a curved apical seta. Anterior occipital row of one or two setae, middle row of 1-4 setae. The interspace between the lowest and the penultimate setae of the posterior occipital row is not much larger than those between the other setae of the row.

Thorax. Pronotum dorsally about as long as pronotal spines. Pronotal ctenidium with 16 spines in male, 14 in female. Arrangement of pseudosetae under mesonotal collar abnormal, see Fig. 43. Metepimeron with about half-a-dozen setae.

Legs. Sulcus of mid coxa dorsally interrupted. Longest apical seta of second hind tarsal segment reaching to the middle of the fourth segment. Three pairs of lateral plantar setae on

fifth hind tarsal segment.

Abdomen. Spiracular fossae of metepimeron and terga II-VII circular or broad oval, that of tergum VIII Y-shaped. More than one seta of tergal main rows below level of tergal spiracular fossae, at least on the anterior terga. Basal sternum with some lateral setae in the

female only. Cuticular ridges of this sternum parallel.

Male (Figs. 67, 99, 161). Sternum VIII with a rounded posterior margin which is partially minutely serrate. Apodeme of tergum IX with an area fusoria in caucasicus only. Corpus of clasper with an internal ventral incrassation in caucasicus only. Fixed process of clasper with at most a rather shallow sinus dividing the dorsal lobe from the ventral lobe; the lower lobe with a small apical seta. Three or four long setae and several shorter ones on fixed process; acetabular seta not quite marginal. Movable process elongate and broadest in the middle; with about 10–15 sensilla along the anterior margin. Fovea elongate or poorly indicated. The four tetrad setae are situated well below the rounded dorso-posterior angle. Distal arm of sternum IX of medium length, apical half of distal arm with a number of short setae and several long ones. Aedeagus dorsally not expanded; lateral wall ventro-posteriorly drawn out into a claw-like lobe; dorso-apical sclerite not very large; hamulus quadrangular and very distinct; median lamella of aedeagal apodeme narrow.

Female (Fig. 204). Posterior margin of sternum VII with a rounded or squarish dorsolateral lobe. Several small setae anterior to the spiracular fossa of tergum VIII. Posterior margin of tergum VIII rounded, without a sinus; apical seta of preventral row well separated from penultimate seta and not placed above the latter; tergum VIII without an unciform sclerotization. Sternum VIII apically broad (in ruris) or pointed (in caucasicus and monticola). Ductus bursae as long as dorsal pronotal spines (in ruris and monticola) or longer (in caucasicus). Spermatheca normal, hilla as long as bulga (in ruris) or shorter (in caucasicus and monticola).

Distribution. South-Eastern Europe.

Hosts. *Spalax* spp.

caucasicus (Taschenberg, 1880), Die Flöhe: 94, pl. 4 figs. 26, 26a. Hungary, Yugoslavia.

ruris Jordan, 1929, Novit. zool. 35: 180, fig. 11. Romania, Yugoslavia. monticola (Kohaut, 1904), Ann. hist.-nat. Mus. hung. 2: 87, fig. A. Yugoslavia.

fissurus-group

Head. Area communis absent in male, present in female. Eye vestigial or fairly distinct. First genal spine almost as long and broad as second from which it is usually separated by a small gap; ratio of spines I: I·2: I·5. Labial palp reaching to $\frac{3}{4}$ length of fore coxa; without apical curved seta. Anterior occipital row of I or 2 setae, middle row of only one seta. Interspace between lowest and penultimate setae of posterior occipital row not much larger than those between the other setae of the row.

Thorax. Pronotum dorsally about as long as pronotal spines. Pronotal ctenidium with 14 (occasionally 15) spines in turcicus and fissurus, 18 in inornatus. Normal arrangement of

mesonotal pseudosetae. Metepimeron with more than 10 setae.

Legs. Sulcus of mid coxa completely interrupted. Longest apical seta of second hind tarsal segment reaching to apex of fourth segment. Three pairs of lateral plantar setae on fifth hind tarsal segment.

Abdomen. Spiracular fossae of metepimeron and terga II—VII almost circular, that of tergum VIII Y-shaped. More than one seta of tergal main rows below level of tergal spiracular

fossae, at least on the anterior terga Basal sternum with or without some lateral setae in

both sexes Cuticular ridges of this sternum parallel

Male (Figs 100, 101, 162, 163) Sternum VIII with a smooth, rounded, posterior margin. Apodeme of tergum IX with an area fusoria. Corpus of clasper with or without a narrow upright internal ventral sclerotization—Fixed process of clasper non-sinuate, with 4–6 long setae and several shorter ones—Movable process elongate triangular, with about ten sensilla along the anterior margin—Fovea elongate or indistinct. Four tetrad setae, situated well below the sclerotized dorso-posterior angle of the movable process. Distal arm of sternum IX a little shorter than proximal arm, with a number of long, slender setae. Aedeagus with a pre-apical dorsal expansion; dorso-apical sclerite long and slender; hamulus rather small and narrow; lateral wall with a ventral lobe pre-apically; median lamella of aedeagal apodeme narrow.

Female (Fig. 205). Posterior margin of sternum VII with a bilobed upper lobe. Some small setae anterior to spiracular fossa of tergum VIII. Posterior margin of tergum VIII broadly rounded; tergum VIII without an unciform sclerotization. Sternum VIII well sclerotized over whole of its length. Ductus bursae shorter than dorsal pronotal spines in fissurus and turcicus, longer in inornatus Spermatheca small, hilla about as long as bulga.

Distribution. ASIA MINOR, CAUCASUS.

This group can be divided into two sub-groups:

fissurus-subgroup

Eye vestigial Pronotal ctenidium with 14 spines in both sexes. Basal sternum with some lateral setae in both sexes Corpus of clasper with an internal ventral sclerotization. Aedeagus without a large ventro-basal sclerotization Ductus bursae shorter than dorsal pronotal spines.

Hosts. Spalax spp.

fissurus Wagner, 1928, Annu. Mus. zool. Acad. St. Pétersb. 30: 29, fig. 8. Asia Minor, Caucasus.

turcicus Jordan, 1946, Proc. R. ent. Soc. Lond., (B) 15:52, figs. 1, 2. Asia Minor.

inornatus-subgroup

Eye clearly indicated. Pronotal ctenidium with 18 spines in both sexes. Basal sternum without lateral setae. Corpus of clasper without internal ventral sclerotization. Aedeagus with a well-developed ventro-basal sclerotization. Ductus bursae longer than dorsal pronotal spines.

Host. Prometheomys schaposchnikowi.

inornatus Wagner, 1916, Bull. Mus. Caucase 10: 56. Asia Minor, Caucasus.

rettigi-group

Head (Fig. 3). Area communis present in both sexes. Eye clearly indicated First genal spine shorter than second and sharply pointed; ratio of spines I: I·3: I·7. Labial palp reaching to $\frac{3}{4}$ length of fore coxa; without a subapical curved seta. Anterior occipital row of two setae, middle row also of two setae.

Thorax. Pronotum as long as or a little shorter than pronotal spines. Pronotal ctenidium with 18 (occasionally 17 or 19) spines in both sexes. Arrangement of pseudosetae under mesonotal collar normal. About half-a-dozen setae on metepimeron.

Legs Sulcus of mid coxa completely interrupted Longest apical seta of second hind tarsal segment reaching at most to middle of segment IV Three pairs of lateral plantar setae on fifth hind tarsal segment.

ENTO. 14, 3. 3.

Abdomen (Fig. 37). Spiracular fossae of metepimeron and terga II—VII small and longish, that of tergum VIII Y-shaped (Fig. 37). One seta (the lowest) of tergal main rows below level

of tergal spiracular fossae. Basal sternum with some lateral setae in female only.

Male (Figs. 52, 105, 106, 164, 165). Sternum VIII with a smoothly rounded posterior margin which is ventrally sinuate. Apodeme of tergum IX without an area fusoria. Corpus of clasper with a narrow upright internal ventral incrassation. Fixed process of clasper broad, with at most a very shallow sinus, the apical seta of the ventral lobe present; the process with three large setae, two of which are in the acetabular area, and a number of smaller marginal setae. Movable process elongate, gradually tapering towards a narrow apex; four or five sensilla along the dorso-anterior margin and a patch of striations at the anterior margin opposite the posterior margin of the fixed process. Fovea absent. Four tetrad setae situated well below apex of movable process. Distal arm of sternum IX of medium length or about as long as proximal arm. Aedeagus without an expansion in the middle of the dorsal margin and without a ventro-basal sclerotization; subapically the dorsal margin bears a papilliform sclerotization; ventro-posterior angle of aedeagal lateral wall produced into a rather narrow lobe; hamulus either large or small; aedeagal apodeme narrow.

Female (Fig. 201). Sternum VII with a large obtuse lateral lobe; with one or a few setae anterior to the spiracular fossa of tergum VIII. Posterior margin of tergum VIII broadly rounded. Tergum VIII anteriorly without unciform sclerotization. Apical short seta of preventral row of tergum VIII not thicker than the slender penultimate one; both setae are marginal and well separated from each other. About a dozen genital setae. Sternum VIII with a broad apex; base of sternum VIII not strongly sclerotized. Ductus bursae at most as long as dorsal spines of pronotal ctenidium. Spermatheca of usual shape, rather small in

acuminatus; hilla shorter than bulga.

Distribution. Romania, Asia Minor, Caucasus.

Hosts. Cricetid rodents.

acuminatus Ioff & Argyropulo, 1934, Z. Parasitenk. 7: 157, figs. 14, 15. Caucasus. rettigi Rothschild, 1908, Proc. zool. Soc. Lond. (1908): 624, pl. 28 figs. 3, 4. Asia Minor, Caucasus, Romania.

triodontus-group

Head (Fig. 13). Area communis present in both sexes. Frontal wall fairly thick. Eye vestigial. First genal spine almost as stout and blunt as the second, from which it is separated by a distinct gap; ratio of spines \eth 1:1·2:1·6, \Diamond 1:1·3:1·7. Labial palp reaching to $\frac{3}{4}$ length of fore coxa or to the apex; without a curved apical seta. Anterior occipital row of 2–4 setae, middle row of three or four setae.

Thorax. Pronotum shorter than length of pronotal spines. Pronotal ctenidium with 16 spines in both sexes. Three or four pseudosetae under mesonotal collar which are often equally

spaced. Metepimeron with more than 10 setae.

Legs. Sulcus of mid coxa completely interrupted. Number of dorso-lateral setal notches in hind tibia varying from 7–9, though seven is the usual number. Longest apical seta of second hind tarsal segment reaching to the apex of fourth segment or a little beyond. Fifth hind tarsal segment with three or four pairs of lateral plantar setae.

Abdomen (Fig. 41). Spiracular fossae of metepimeron and terga II-VII circular or broad oval, that of tergum VIII Y-shaped (Fig. 41). More than one seta of tergal main rows below level of tergal spiracular fossae. Basal sternum of female with lateral setae (in edwardsi and

audax) or without (in triodontus); cuticular ridges of this sternum finger-print-like.

Male (Figs. 108–110, 166–168). With 1–5 setae anterior to spiracular fossa of tergum VIII. Sternum VIII with a rounded smooth posterior margin. Apodeme of tergum IX with an area fusoria. Corpus of clasper with at most a relatively small internal ventral incrassation. Fixed process of clasper with 3–5 marginal or submarginal setae and one acetabular seta, which

is separated by a wide gap from the other large setae in *triodontus* only, and without a developed upper lobe; ventral lobe with a longish dorso-apical seta. Movable process triangular or elongate, with 5–10 sensilla along the anterior (apical) margin. Fovea absent. Four tetrad setae in *triodontus* and *edwardsi*, 6–7 in *audax*; these setae are situated at the dorso-posterior angle in *edwardsi* and a little below this angle in *triodontus* and *audax*. Dorso-posterior angle of movable process sclerotized. Distal arm of sternum IX of medium length, with at least some of its setae longish. Aedeagus with a very large triangular dorso-apical sclerite and with the apical part of the ventral margin of the lateral wall divided by a wide sinus into two pointed lobes; median lamella of aedeagal apodeme narrow.

Female (Fig. 207). Posterior margin of sternum VII with a rather large dorso-lateral lobe. No setae anterior to spiracular fossa of tergum VIII. Posterior margin of tergum VIII with at most a rather shallow sinus. Ventro-posterior setae of tergum VIII marginal except in audax where they are placed some distance away from the margin. Tergum VIII without an unciform sclerotization. Apex of sternum VIII acute in triodontus and audax, broadly rounded in edwardsi. Ductus bursae about as long as dorsal spines of pronotal ctenidium in triodontus and edwardsi, longer than those spines in audax. Hilla of spermatheca shorter than bulga; spermatheca normal.

Distribution. East Africa.

Hosts. Tachyoryctes spp.

audax Jordan & Rothschild, 1913, Novit. 2001. 20: 546, 549, 560, figs. 17, 18. Kenya. edwardsi Jordan, 1937, Novit. 2001. 40: 329, figs. 102, 103. Kenya.

triodontus Rothschild, 1907, Novit. zool. 14: 330, figs. 2, 3 [not fig. 4; see 1912, Novit. zool. 19: 365, footnote]. Presumably East Africa.

particularis-group

Head (Fig. 18). Area communis present in both sexes. Eye vestigial. Spines of genal ctenidium relatively large, the first two bluntly tipped; ratio of spines 1:1.5:1.8. Labial palp reaching to about middle of fore coxa; without a curved apical seta. Frontal row of five or six setae. Anterior and middle occipital rows each with two setae.

Thorax (Figs. 18, 19). Pronotum expanded dorso-apically; pronotal ctenidium of 12 curved spines in both sexes, the two lowest of which are the longest; ctenidium distinctly curved, specially so in the female and all spines point downwards and backwards. Two subdorsal pseudosetae and one in the middle of the mesonotal collar. About half-a-dozen setae on metepimeron.

Legs. Sulcus of mid coxa complete. Longest apical seta of second hind tarsal segment reaching to about two-thirds of third segment. Four pairs of lateral plantar setae on fifth hind tarsal segment.

Abdomen. Spiracular fossae of metepimeron and terga II-VII conical, that of tergum VIII Y-shaped but fairly broad basally. One seta (the lowest) of tergal main rows below level of tergal spiracular fossae. Basal sternum without lateral setae.

Male (Figs. 58, 107, 170). Sternum VIII with a smooth posterior margin and a ventral sinus (Fig. 58). Apodeme of tergum IX narrow, without an area fusoria. Corpus of clasper without a projecting internal ventral incrassation. Fixed process of clasper with a shallowly concave posterior margin, dorsally with one long and several shorter setae; one acetabular seta. Movable process spindle-shaped, with four hair-like sensilla at the apex and four very small tetrad setae at the middle of the posterior margin. Fovea circular. Distal arm of sternum IX of medium length, with about half-a-dozen long and slender apical setae and several shorter preapical ones. Aedeagus without a dorsal expansion and without a ventro-basal sclerotization; dorso-apical sclerite elongate; lateral wall with curved striae and sinuate ventro-posteriorly; aedeagal apodeme narrow.

Female (Fig. 209). Sternum VII with a broad and straight lateral lobe. No setae anterior to spiracular fossa of tergum VIII. Posterior margin of tergum VIII with a rounded lobe; anteriorly without unciform sclerotization. Apical seta of tergum VIII long. Sternum VIII very narrow, with a pointed apex; base of sternum VIII not strongly sclerotized. Ductus bursae shorter than dorsal spines of pronotal ctenidium. Bulga of spermatheca relatively very small, about as long as hilla.

Distribution. Eastern Congo and N.E. Tanganyika.

Hosts. Soricid insectivores?

particularis Berteaux, 1949, Rev. Zool. Bot. afr. 41: 343, figs. 1–3. Eastern Congo Republic (Kivu), N.E. Tanganyika.

pseudagyrtes-group

Head. Area communis absent in male, present in female, eye clearly indicated. First genal spine a little shorter and narrower than second; ratio of spines $3 : 1 \cdot 1 : 1 \cdot 4, 9 : 1 \cdot 2 : 1 \cdot 5$. Labial palp reaching to $\frac{3}{4}$ (or a little beyond) length of fore coxa; with a curved apical seta. Anterior occipital row of two setae, middle row of three and the interspace between the upper two is smaller than between the lower two.

Thorax. Pronotum shorter than length of pronotal spines. Pronotal ctenidium with 16 spines in male (sometimes 14?), 14 in female. Normal arrangement of pseudosetae under

mesonotal collar. About half-a-dozen setae on metepimeron.

Legs. Sulcus of mid coxa complete. Longest apical seta of second hind tarsal segment reaching to about apex of third segment. Three pairs of lateral plantar setae on fifth hind tarsal segment but four pairs in *expansus*.

Abdomen. Spiracular fossae of metepimeron and terga II-VII conical, the one on tergum VIII Y-shaped. One seta (the lowest of the tergal main rows) below level of tergal spiracular

fossae. Basal sternum without lateral setae.

Male (Figs. 53, 102, 169). Tergum VIII with one or a few setae anterior to spiracular fossa; sternum VIII with a partially finely serrate posterior margin which tapers to a rounded ventro-posterior angle. Apodeme of tergum IX without an area fusoria. Corpus of clasper with a triangular internal ventral incrassation. Fixed process of clasper divided by a fairly wide sinus into two lobes, the lower of which is not sinuate. Dorsal lobe of fixed process with three to five large setae. Ventral lobe of this process with a small dorso-apical seta. Movable process elongate or spindle-shaped. Antero-dorsal margin of this process rounded, without a distinct angle, along this margin five to ten sensilla. Fovea oval. Four tetrad setae, situated well below apex of movable process. Dorso-posterior angle of movable process usually sclerotized. Distal arm of sternum IX of medium length or about as long as proximal arm, with at least some of its setae longish. Aedeagus without a median dorsal expansion and without a ventro-basal sclerotization; aedeagal apodeme narrow.

Female (Fig. 202). Sternum VII bilobed or with a single large lateral lobe. No setae anterior to spiracular fossa of tergum VIII. Posterior margin of tergum VIII broadly rounded. Tergum VIII anteriorly without an unciform sclerotization. The apical seta of preventral row of tergum VIII not stouter than penultimate seta and placed obliquely above the latter. Sternum VIII with a short sclerotized narrow apex; base of sternum VIII not strongly sclerotized. Ductus bursae about as long as or longer than dorsal pronotal spines. Sperma-

theca of normal shape and size, hilla shorter than bulga.

Distribution. Nearctic Region.

Hosts. Small rodents (Murinae, Microtinae).

caballeroi Barrera & Machado, 1960, Homenaje Dr. E. Caballero y C.: 549, figs. 1-4. Mexico.

expansus Traub, 1950, Fieldiana, Zool. Mem. 1:70, pl. 41 figs. 1-5. Mexico.

haagi Traub, 1950, Fieldiana, Zool. Mem. 1:68, pl. 40 figs. 1-11. Mexico.

pseudagyrtes pseudagyrtes Baker, 1904, Proc. U.S. nat. Mus. 27: 420, 421, pl. 11, figs. 7–12. North America (westward to the Rocky Mountains).

pseudagyrtes micropus Traub, 1950, Fieldiana, Zool. Mem. 1:73, pl. 43, figs. 4, 7–9. Mexico.

sanborni Traub, 1950, Fieldiana, Zool. Mem. 1:72, pl. 42, figs. 1–11. Guatemala and El Salvador.

moratus-group

Head (Fig. 12). Area communis present in both sexes. Eye well-developed, dark. Frons with a marginal short seta in a notch just above the oral angle. First genal spine a little shorter and narrower than second; ratio of spines I: I·4: I·7. Labial palp not reaching beyond two-thirds length of fore coxa; without a curved apical seta. Anterior occipital row of three (occasionally four) setae, middle row of 3–5 setae.

Thorax. Pronotum dorsally about as long as pronotal spines. Pronotal ctenidium with 16 spines in both sexes. Normal arrangement of mesonotal pseudosetae. About half-a-dozen

setae on metepimeron.

Legs. Sulcus of mid coxa complete. Longest apical seta of second hind tarsal segment reaching at most to just over apex of third segment. Fifth hind tarsal segment with four pairs of lateral plantar setae (occasionally three on one side in *moratus*).

Abdomen. Spiracular fossae of metepimeron and terga II-VII conical, that of tergum VIII Y-shaped. One seta (the lowest) of tergal main rows below level of tergal spiracular fossae.

Basal sternum without lateral setae.

Male (Figs. 111, 171). Tergum VIII with 3–5 setae anterior to spiracular fossa. Sternum VIII with a smooth, rounded or broadly truncate posterior margin. Apodeme of tergum IX with an area fusoria. Corpus of clasper with a triangular internal ventral incrassation. Fixed process of clasper divided by a shallow sinus into two lobes; with 3–4 stout setae and a marginal acetabular seta; ventral lobe without a small dorso-apical seta. Movable process elongate and widest in the middle; with 10–14 sensilla along anterior margin and dorso-anterior angle; three tetrad setae, of which the upper one is very short and the middle one long, placed well below dorso-posterior angle; margin of movable process immediately above tetrad setae angular and strongly sclerotized, dorso-posterior angle also markedly sclerotized. Fovea elongate. Distal arm of sternum IX variable in length, from very short to medium, with several long setae. Aedeagus without a dorsal expansion in the middle; dorso-apical sclerite very long; no ventro-basal sclerotization; aedeagal apodeme relatively very broad.

Female (Fig. 210). Sternum VII with an entire or sinuate dorsal lobe. Anterior to spiracular fossa of tergum VIII 1–4 small setae. Posterior margin of tergum VIII without a sinus. Tergum VIII anteriorly with or without an unciform sclerotization. None of the setae of tergum VIII marginal. Sternum VIII long and narrow, its posterior half well sclerotized. Ductus bursae much longer than dorsal pronotal spines. Spermatheca of normal shape and size; hilla longer than bulga.

Distribution. West Africa.

Hosts. Murid rodents.

moratus Jordan, 1926, Novit. zool. 33: 393, figs. 20–22. Ghana. acunus Jordan, 1929, Novit. zool. 35: 166, figs. 2, 4. Nigeria. tertius Smit, 1960, Tijdschr. Ent. 103: 281, figs. 8–11. Ivory Coast.

atomus-group

Head. Area communis present in both sexes. Eye fairly well-developed, dark. First genal spine shorter and narrower than second; ratio of spines $3 : 1 \cdot 4 : 1 \cdot 7$, $9 : 1 \cdot 6 : 1 \cdot 9$. Labial palp reaching to two-thirds length of fore coxa; without a curved apical seta. Anterior occipital row of 2-4 setae, middle row of three or four.

Thorax. Pronotum markedly shorter than length of pronotal spines. Pronotal ctenidium with 16 spines in both sexes. Normal arrangement of mesonotal pseudosetae. About half-a-

dozen setae on metepimeron.

Legs. Sulcus of mid coxa complete. Longest apical seta of second hind tarsal segment reaching almost to or beyond apex of third segment. Three or four lateral plantar setae per side on fifth hind tarsal segment.

Abdomen. Spiracular fossae of metepimeron and terga II-VII conical, that of tergum VIII Y-shaped. One seta (the lowest) of tergal main rows below level of tergal spiracular fossae.

Basal sternum without lateral setae.

Male (Figs. 60, 112, 172). Tergum VIII with 3–5 setae anterior to spiracular fossa. Sternum VIII with ventral margin slightly folded, posterior margin smooth but with minute "scales" along it in ominosus. Area fusoria of apodeme of tergum IX very small or absent. Corpus of clasper with an upright and fairly narrow internal ventral incrassation. Fixed process of clasper with a thin acetabular extension, bearing the acetabular seta which is thus placed distantly from the four stout setae on the fixed process; the very short ventral lobe with or without a small dorso-apical seta. Movable process rather broad, with an obliquely truncate apex; inner surface of ventro-posterior half of movable process minutely spiculose; along anterior margin of this process 9–12 sensilla; fovea elongate; five or six tetrad setae, three of which are large, placed not far below non-sclerotized dorso-posterior angle. Upper part of proximal arm of sternum IX relatively very narrow; distal arm of medium length or about as long as proximal arm, with a number of short and very short setae. Aedeagus dorsally concave; dorso-apical sclerite very narrow and almost inapparent; no ventro-basal sclerotization; hamulus large and well sclerotized; aedeagal apodeme straight and rather narrow.

Female (Fig. 211). Posterior margin of sternum VII with a dorsal and lateral lobe which are separated by a conspicuous sinus. Above spiracular fossa of tergum VIII 3–5 small setae. Posterior margin of tergum VIII with at least an indication of a lateral sinus. Tergum VIII anteriorly without an unciform sclerotization. The two most posterior setae on the outer side of tergum VIII, above the ventro-posterior angle, are marginal. Sternum VIII narrow and well defined. Ductus bursae shorter than dorsal pronotal spines. Sperma-

theca normal, hilla shorter than bulga.

Distribution. Angola and southern part of Congo.

Hosts. Murid rodents.

atomus Jordan & Rothschild, 1913, Novit. zool. 20: 551, fig. 22. Angola. ominosus Smit, 1959, Rev. Zool. Bot. afr. 60: 326, figs. 1–5. Congo (Katanga).

evidens-group

Head. Area communis present in both sexes. Eye fairly well-developed. First genal spine shorter and narrower than second; ratio of spines $3 \text{ i} : 1 \cdot 2 : 1 \cdot 6$, $2 \text{ i} : 1 \cdot 3 : 1 \cdot 6$. Labial palp reaching to two-thirds (evidens sspp.) or $\frac{3}{4}$ (acanthurus, lycosius) length of fore coxa; without a curved apical seta. Anterior occipital row with 3-5 setae, middle row also of 3-5 setae.

Thorax. Pronotum dorsally shorter than pronotal spines. Pronotal ctenidium with 16 spines in both sexes. Normal arrangement of mesonotal pseudosetae. About half-a-dozen

setae on metepimeron.

Legs. Sulcus of mid coxa complete. Longest apical seta of second hind tarsal segment reaching to apex of third segment or to middle of fourth. Fifth hind tarsal segment with three or four pairs of lateral plantar setae in *lycosius* and *evidens*, four pairs in *acanthurus*.

Abdomen. Spiracular fossae of metepimeron and terga II-VII conical, the one of tergum VIII Y-shaped. One seta (the lowest) of tergal main rows below level of tergal spiracular fossae. Basal sternum without lateral setae.

Male (Figs. II3–II5, I73–I75). Tergum VIII with a small number of setae anterior to spiracular fossa. Ventral margin of sternum VIII indented. Apodeme of tergum IX with an area fusoria (sometimes very small). Corpus of clasper with a triangular internal ventral incrassation in evidens and lycosius, without one in acanthurus. Fixed process of clasper divided by a very shallow sinus into two lobes, the lower of which has a small dorso-apical seta in lycosius only; the process with 3–5 large setae. Movable process widest apically; about half-a-dozen sensilla along dorso-anterior angle; four tetrad setae situated just below dorso-posterior angle of movable process. Fovea very long and narrow and well sclerotized. Distal arm of sternum IX about as long as proximal arm, with short setae only, while in acanthurus the apical portion of the ventral margin also bears a short row of dark spiniform setae. Lateral wall of aedeagus forming posteriorly a narrow and pointed process, except in acanthurus; dorso-apical sclerite of medium length and fairly broad; no ventro-basal sclerotization; aedeagal apodeme of medium width.

Female. Posterior margin of sternum VII with a dorsal, or a dorsal and ventral, lateral lobe. With or without setae anterior to spiracular fossa of tergum VIII. Posterior margin of tergum VIII sinuate. Tergum VIII anteriorly without an unciform sclerotization. Ventro-posterior setae of tergum VIII marginal. Sternum VIII with a broad apex. Ductus bursae shorter than dorsal pronotal spines. Hilla of spermatheca longer than bulga in lycosius, shorter in

evidens and acanthurus.

Distribution. East Africa.

Hosts. Murid rodents.

evidens evidens Jordan, 1929, Novit. zool. 35: 165, figs. 1, 3. Eastern Congo, Uganda. evidens elgonensis Jordan, 1938, Novit. zool. 41: 114, fig. 58. Uganda (Mt. Elgon). evidens modicus Jordan, 1933, Novit. zool. 38: 349, figs. 68, 70. Kenya.

acanthurus Jordan & Rothschild, 1913, Novit. 2001. 20: 551, figs. 23, 24. Kenya,

Tanganyika.

lycosius Jordan & Rothschild, 1913, Novit. 200l. 20: 554, fig. 25 (the described female, fig. 26, is that of eumeces; see Jordan, 1936, Novit. 200l. 39: 301). Kenya.

calceatus-group

Head. Area communis present in both sexes. Eye well-developed, dark. First genal spine distinctly shorter and narrower than second; ratio of spines $i:i\cdot 4:i\cdot 8$. Labial palp reaching to two-thirds length of fore coxa; without a curved apical seta. Anterior occipital row with three or four setae, middle row of four setae (occasionally three).

Thorax. Pronotum dorsally shorter than pronotal spines. Pronotal ctenidium with 16 spines in both sexes. Normal arrangement of mesonotal pseudosetae. About half-a-dozen setae

on metepimeron.

Legs. Sulcus of mid coxa complete. Longest apical seta of second hind tarsal segment reaching to about the apex of the third segment. Fifth hind tarsal segment with three or four lateral plantar setae per side.

Abdomen. Spiracular fossae of metepimeron and of terga II-VII conical, that of tergum VIII Y-shaped. One seta (the lowest) of tergal main rows below level of tergal spiracular fossae.

Basal sternum without lateral setae.

Male. (Figs. 59, 116, 117, 179, 180). Tergum VIII with 4-6 setae anterior to spiracular fossa. Sternum VIII with a rounded posterior margin which is ventrally minutely serrate (except in ansorgei) and has the appearance of being folded over in calceatus and ansorgei. Apodeme of tergum IX with an area fusoria in bacopus only. Corpus of clasper with a narrow upright

internal ventral sclerotization. Fixed process of clasper markedly sinuate, the dorsal lobe with 3-4 large setae, ventral lobe without a small apical seta. Movable process broad; with 12-20 sensilla along anterior margin; with 5-7 tetrad setae placed a short distance below dorso-posterior angle of movable process; fovea elongate or ovoid. Distal arm of sternum IX of medium length and with short setae only. Aedeagus with conspicuous dorso-posterior extension (except in bacopus); dorso-apical sclerite long or very long; hamulus large and well defined; lateral wall with a ventral sclerotization; aedeagal apodeme straight and rather narrow.

Female. Posterior margin of sternum VII with a dorsal and a ventral lobe or with only a sinuate dorsal lobe. Anterior to spiracular fossa of tergum VIII 2–6 small setae. Posterior margin of tergum VIII sinuate. Tergum VIII anteriorly without an unciform sclerotization. Ventro-posterior setae of tergum VIII marginal. Sternum VIII narrow, with a pointed apex, sclerotized over whole of its length. Ductus bursae shorter than dorsal pronotal spines. Hilla of spermatheca shorter than bulga except in bacopus and allisoni in which the two are of

subequal length.

Distribution. Southern and Eastern Africa.

Hosts. Murid rodents.

allisoni Smit, 1962, Rev. Zool. Bot. afr. 66: 200, figs. 9-12. Ethiopia.

ansorgei ansorgei Rothschild, 1907, Novit. 2001. 14: 330, fig. 4 (not fig. 2). Angola, S.W. Congo, Nyasaland.

ansorgei catanganus Jordan, 1936, Novit. 2001. 39: 295, fig. 52. Congo (Katanga, Maniema).

bacopus Jordan, 1933, Novit. 200l. 38: 350, figs. 69, 71. Uganda, Congo, Central African Republic.

calceatus calceatus Waterston, 1912, Ent. mon. Mag. 48: 27, 1 fig. South-eastern Africa.

calceatus cabirus Jordan & Rothschild, 1913, Novit. 2001. 20: 549, figs. 20, 21 Eastern Africa.

natalensis Marcus & de Meillon, 1960, Novos Taxa ent. 22: 6, pl. 2 figs. 1-4. Natal.

eumeces-group

Head. Area communis present in both sexes. Eye apparently more or less vestigial in *stenurus*, but well developed and dark in the other species of this group. First genal spine shorter and narrower than second; ratio of spines $3 : 1 \cdot 3 : 1 \cdot 3 : 1 \cdot 3 : 1 \cdot 6$. Labial palp not reaching beyond two-thirds length of fore coxa; without a curved apical seta. Anterior occipital row with 2-4 setae, middle row with 3-4 setae.

Thorax. Pronotum dorsally as long as or shorter than pronotal spines. Pronotal ctenidium with 16 spines in both sexes. Normal arrangement of mesonotal pseudosetae. About half-a-

dozen setae on metepimeron.

Legs. Sulcus of mid coxa complete. Longest apical seta of second hind tarsal segment not quite reaching or reaching a little beyond apex of third segment. Fifth hind tarsal segment with four (occasionally three) pairs of lateral plantar setae.

Abdomen. Spiracular fossae of metepimeron and terga II-VII conical, that of tergum VIII Y-shaped. One seta (the lowest) of tergal main rows below level of tergal spiracular fossae.

Basal sternum without lateral setae.

Male (Figs. 118, 119, 176–178). Tergum VIII with 2–6 setae anterior to spiracular fossa. Sternum VIII normal, with upper part of posterior margin finely serrated. Apodeme of tergum IX with an area fusoria. Corpus of clasper with a triangular or elongate internal ventral sclerotization. Fixed process entire or only lower lobe differentiated, the latter without a small dorso-apical seta; the process with 4–6 large setae and one acetabular seta which is not separated by a wide gap from the other large setae. Movable process long and narrow (except

in *nyikensis*) and often angular; with 5–11 sensilla along anterior margin; 3–5 tetrad setae situated well below dorso-posterior angle; fovea circular or elongate; with or without a small circular sclerotization above tetrad setae; dorso-posterior angle of movable process little or well sclerotized. Distal arm of sternum IX as long as proximal arm or nearly so, with several of its setae fairly long. Lateral wall of aedeagus forming dorso-posteriorly a usually pointed process; dorso-apical sclerite very slender; no ventro-basal sclerotization; aedeagal apodeme narrow.

Female. Posterior margin of sternum VII with a sinuate dorso-lateral lobe. Anterior to spiracular fossa of tergum VIII o-2 (occasionally three) setae; posterior margin of tergum VIII forming a dorsal lobe; tergum VIII anteriorly with or without an unciform sclerotization; apical setae of preventral row marginal. Sternum VIII long and narrow, its posterior half well sclerotized. Ductus bursae not strongly sclerotized and shorter than dorsal pronotal spines. Hilla of spermatheca about as long as, or a little longer than, the bulga.

Distribution. East Africa.

Hosts. Murid rodents.

blandulus Smit, 1960, Ann. Mus. Congo, Zool. 88: 359, figs. 25–28. Tanganyika. eumeces Jordan & Rothschild, 1913, Novit. zool. 20: 548, fig. 19. Eastern Congo, Uganda, Kenya.

flagellatus Smit, 1963, Rev. Zool. Bot. afr. 67 (in press). Nyasaland. nyikensis Smit, 1962, Rev. Zool. Bot. afr. 66: 197, figs. 6–8. Nyasaland. stenurus Jordan, 1937, Novit. zool. 40: 329, fig. 101. Kenya. verutus Smit, 1960, Ann. Mus. Congo, Zool. 88: 362, figs. 29, 30. Tanganyika.

eximius-group

Head. Area communis present in both sexes. Eye fairly well-developed. First genal spine narrower and a little shorter than second; ratio of spine δ 1: 1·2: 1·5, φ 1: 1·2: 1·6. Labial palp reaching to two thirds length of fore coxa; without a curved apical seta. Anterior occipital row with two setae, middle row with three.

Thorax. Pronotum dorsally considerably shorter than pronotal spines. Pronotal ctenidium with 16 spines in both sexes. Normal arrangement of mesonotal pseudosetae. About half-adozen setae on metepimeron.

Legs. Sulcus of mid coxa completely interrupted. Longest apical seta of second hind tarsal segment reaching to about apex of third segment or a little beyond. Fifth hind tarsal segment with three pairs of lateral plantar setae.

Abdomen. Spiracular fossae of metepimeron and terga II-VII conical, that of tergum VIII Y-shaped. One seta (the lowest) of tergal main rows below level of tergal spiracular fossae. Basal sternum without lateral setae.

Male (Figs. 120, 181). Tergum VIII with 3-4 setae anterior to spiracular fossa. Sternum VIII triangular, with a straight and finely serrate posterior margin. Apodeme of tergum IX with a small area fusoria. Corpus of clasper with a very small horizontal internal ventral incrassation. Fixed process with at most a shallow sinus, with two very strong setae apart from the more slender acetabular seta. Movable process elongate and widest apically; with about half-a-dozen thin sensilla along dorso-anterior angle; with only two tetrad setae, placed a short distance below the well sclerotized dorso-posterior angle; fovea absent. Distal arm of sternum IX rather short, with one strong and several shorter setae. Aedeagus not strongly modified; lateral wall posteriorly rounded; dorso-apical sclerite narrow; hamulus narrow and distinct; no ventro-basal sclerotization; aedeagal apodeme fairly narrow.

Female (Fig. 206). Tergum VII normally with 4 (occasionally 3 or 5) stout antesensilial setae each side. Posterior margin of sternum VII with a long sinuate lateral lobe. Anterior to spiracular fossa of tergum VIII 2-3 small setae. Posterior margin of tergum VIII without a

sinus; tergum VIII anteriorly with an unciform sclerotization; none of the setae of tergum VIII marginal. Sternum VIII short and fairly narrow, not strongly sclerotized. Ductus bursae a little shorter or about as long as dorsal pronotal spines. Hilla of spermatheca shorter than bulga.

Distribution. East Africa.

Hosts. Murid rodents.

eximius Jordan & Rothschild, 1913, Novit. 2001. 20: 558, figs. 29, 30. Eastern Congo, Uganda, Kenya, Tanganyika, Nyasaland.

UNGROUPABLE ETHIOPIAN SPECIES

I have been unable, for the time being, to group the Ethiopian species listed below. Segment IX of the male and the phallosome are figured.

arcanus Smit, 1960, Tijdschr. Ent. 103: 283, figs. 12–14. Angola. (Figs. 122, 183.)

cophurus Jordan & Rothschild, 1913, Novit. 2001. 20: 556, figs. 27, 28. East Africa. (Figs. 121, 182.)

debrauwerei Berteaux, 1949, Rev. Zool. Bot. afr. 41: 345, figs. 4, 5. Congo. (Figs. 124, 188.)

devignati Jordan, 1941, Proc. R. ent. Soc. Lond. (B) 10:43, fig. 1. Congo. (Figs. 125, 190.)

engis Rothschild, 1907, Ent. mon. Mag. 43: 176, pl. 3, fig. 3. Ethiopia.

luberensis Berteaux, 1949, Rev. Zool. Bot. afr. 41: 346, figs. 6, 7. Congo. (Figs. 129, 185.)

olbius Jordan & Rothschild, 1923, Ectoparasites 1: 306, figs. 306, 307. Kenya.

phyris Jordan, 1941, Proc. R. ent. Soc. Lond. (B) 10: 45, figs. 2, 3. Congo. (Figs. 126, 184.)

singularis Jordan, 1936, Novit. 2001. 39: 302, figs. 64-66. Uganda. (Figs. 123, 186.)

smithersi De Meillon, 1950, J. ent. Soc. sthrn. Afr. 13:35, figs. 1a, b, c. S. Rhodesia. (Figs. 128, 189.)

vanhooft Berteaux, 1947, Rev. Zool. Bot. afr. 40: 97, figs. 2, 3. Congo. (Figs. 127, 187.)

LIST OF SYNONYMS AND OTHER NOMENCLATURAL CHANGES

adetus Jordan & Rothschild, 1920, Ectoparasites 1: 106, fig. 96 = bisoctodentatus bisoctodentatus Kolenati, 1863. Syn. nov.

agyrtes bosnicus Wagner, 1930, Acta ent. Soc. jugoslav. 3–4:40, fig. 5 = agyrtes serbicus Wagner, 1930. Syn. nov.

agyrtes carnicus Rosický & Carnelutti, 1959, Čsl. Parasitol. 6: 137, figs. 2, 3A, 6D = agyrtes wagnerianus Peus, 1950. Syn. nov.

agyrtes celticus Jordan & Rothschild, 1922, Ectoparasites 1:282 = nobilis nobilis (Rothschild, 1898) (see Thompson, 1935, Ent. mon. Mag. 71:257).

agyrtes hadzii Rosický & Carnelutti, 1959, Čsl. Parasitol. 6: 140, figs. 3B, 3C, 4, 5, 6A-C = agyrtes serbicus Wagner, 1930. Syn. nov.

agyrtes hanzaki Rosický, 1950, Prirodov. Sb. 5: 163, fig. 4 = agyrtes agyrtes (Heller, 1896). Syn. nov.

agyrtes jiroveci Rosický, 1955, Zool. ent. Listy 4: 367, figs. 1B, C = agyrtes peusianus

Rosický, 1955. Syn. nov.

agyrtes jordanianus Peus, 1950, Syllegomena biol., Festschr. Kleinschmidt: 292, fig. 3D = agyrtes graecus Jordan, 1926. Syn. nov.

agyrtes kraljevensis Wagner, 1930, Acta Soc. ent. jugoslav. 3-4:39, fig. 4 = agyrtes serbicus Wagner, 1930. Syn. nov.

agyrtes noster Ioff, 1953, Med. Parazitol., Moskva 22: 462 = agyrtes kleinschmidtianus Peus, 1950. Syn. nov.

agyrtes obenbergeri Rosický, 1957, Čsl. Parasitol. 4: 294, figs. 1, 2 = agyrtes peusianus Rosický, 1954. Syn. nov.

agyrtes oreadis Jordan & Rothschild, 1920, Ectoparasites 1: 104, figs. 90-93 = agyrtes verbanus Jordan & Rothschild, 1920. Syn. nov.

agyrtes slovacicus Rosický, 1950, Prirodov. Sb. 5: 163, figs. 1-3 = agyrtes agyrtes = agyrtes peusianus. Syn. nov.

agyrtoides Wahlgren, 1911, Ent. Tidskr. 32: 105, figs. 1, 2 = agyrtes agyrtes (Heller, 1896). Syn. nov.

bisoctodentatus occidentalis Smit, 1956, Ent. mon. Mag. 92: 296 = bisoctodentatus heselhausi (Oudemans, 1914) (see Smit, 1962, Tijdschr. Ent. 105: 56).

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bogatschevi Wagner & Argyropulo, 1934—a subspecies of congener.

calceatus cabirus Jordan & Rothschild, 1913—Comb. nov. for cabirus.

calceatus septentrionalis de Meillon, 1940, J. ent. Soc. sthrn Afr. 3:62, figs. 1, 2 = calceatus [calceatus] Waterston, 1912 (see de Meillon, 1950, l. c. 13:35).

campestris Peus, 1949, Z. Parasitenk. 14:96, figs. 7, 8 = assimilis (Taschenberg, 1880). Syn. nov.

congener bulgaricus Rosický, 1959, Acta Acad. Sci. czechoslov. brun. 31: 332, figs. 11, 12B, 12C = congener vicarius Jordan & Rothschild, 1921. Syn. nov.

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hispanicus Jordan, 1938—a full species, not a subspecies of agyrtes.

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obtusus recurvus Peus, 1951, Veštn. Čsl. zool. spol. 15: 236, figs. 2, 4, 5 = obtusus

Jordan & Rothschild, 1912. Syn. nov.

orientalis kratochvili Jurík, 1955, Acta Univ. Agric. Brno (1955): 176, fig. 2 = orientalis (Wagner, 1898) (see Rosický, 1957, Fauna ČSR 10: 242).

orphilus heinrichi Peus, 1949, Z. Parasitenk. 14:98, figs. 9, 10b, 11c = orphilus dolomiticus Jordan, 1928. Syn. nov.

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phrator Jordan, 1929, Novit. 2001. 35: 180, figs. 12, 13 = inornatus Wagner, 1916 (see Ioff & Argyropulo, 1934, Z. Parasitenk. 7: 157).

ruris karamani Wagner, 1936, Z. Parasitenk. 8: 349, figs. 21, 22 = ruris Jordan, 1929. Syn. nov.

russulae ducis Jordan, 1929, Novit. 2001. 35: 41, fig. 3 = russulae Jordan & Rothschild,

1912. Syn. nov.

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